ECOLOGY

VOL. 38 APRIL, 1957 No. 2

THE USE OF CO^{60} AS A TAG FOR RECOVERING AMPHIBIANS IN THE FIELD[1]

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INTRODUCTION

Students of amphibian and reptile ecology are often vexed by the problem of determining where animals go following periods of observable activity. It is generally known that nearly all amphibian and reptile species retreat underground, but where and how deep are usually unanswered questions. Random excavation of suspected subterranean niches is usually an uncertain procedure. Many of the available data on aestivating or hibernating forms have come from chance observations or when special opportunities present themselves. Cowles (1941) utilized the chance afforded by a land clearing project to gather hibernation data on desert reptiles unearthed by a tractor and scraper. Oliver (1955) reports Latham's observations on Fowler's toad, *Bufo woodhousi fowleri,* plowed up in fields on Long Island, New York. Many other bits of information are scattered throughout the literature, but the fact remains that critical data on the retreat site and physiological condition of hibernating animals are usually absent from life history studies.

Tagging animals with a radioactive isotope and detection with suitable instruments is a relatively new technique which has been used to advantage in field studies of mosquitoes (Hassett and Jenkins 1949; Bugher and Taylor 1949), click beetles (Brian 1947), plovers (Griffin 1952), field voles (Godfrey 1954), and moles (Godfrey 1955). Lachelt (1954) has suggested possible uses of radioactive isotopes in wildlife investigations where the transmission of radioactivity by animals in close association with each other might be used in studying mother-young or prey-predator-scat relationships.

[1] The method herein reported was worked out as one means of gathering data for the author's completed doctoral dissertation on the ecology and systematics of the genus *Bufo* in the Sierra Nevada of California. Author's present address: Department of Biology, Augustana College, Rock Island, Illinois.

The author has been engaged in a study of the natural history of the Yosemite toad, *Bufo canorus* Camp, a species occupying elevations between 7000 and 11,000 feet in the Sierra Nevada of east-central California. In an attempt to recover toads in their subterranean retreats part of a population was tagged with radioactive cobalt during the late spring and summer of 1955. A description of the methods and problems involved and some of the results are herein reported.

Grateful acknowledgment is made of the facilities and detection equipment made available by the Radiation Safety Division, University of California, Berkeley. Horton Steel suggested the use of the radioactive method in tagging amphibians. Special thanks are due Robert Magill, Radiation Safety Engineer, for his helpful advice and active interest in the project. Dr. Robert C. Stebbins and Dr. Oliver P. Pearson kindly read the manuscript and offered valuable suggestions.

MAKING THE TAGS

Standard metal leg tags have been modified successfully for use in radioactive tagging work by Griffin on birds and Godfrey on small mammals. Marking toads with metal jaw tags has proved less successful due to the impermanency of the tags (Stille 1950). Subcutaneous tags were employed in this study. The use of lead in making capsules has two advantages: (1) ease of shaping and handling and (2) the shielding of the animal from beta rays, which are not of significant value in detection but which could cause serious tissue damage. Heavy plastic coating of the lead is designed to prevent possible poisonous effects of the heavy metal and the radioisotope. In later experiments the author placed the lead tags in biologically safe polyethylene tubing and heat-fused the ends. This latter method might insure greater protection to the toad than relying on total coverage of the lead with plastic spray.

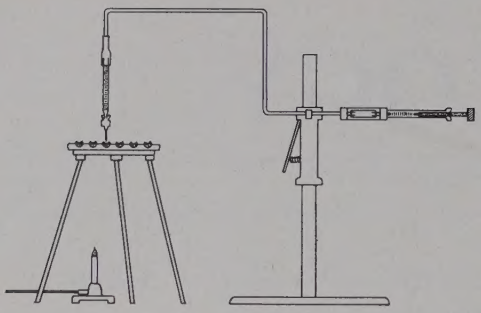

FIG. 1. Remote pipetter apparatus used to allocate Co^{60} ($CoCl_2$) to the lead shot used as tags.

Fisherman's split-shot sinkers (Pflueger size 3-0) are hollowed out with an electric drill. After the rough edges have been filed, the shot are arranged on a punched metal depression plate which rests on a tripod stand. The remote pipetter (Fig. 1) provides a safe and convenient way to allocate unit quantities of Co^{60} in solution to each shot by the drop method. The fraction of a milliliter of solution contained in a single drop is volumetrically determined. Using this figure, it is simple to calculate the approximate radioactivity contained in a single drop of cobalt chloride solution of known concentration. Gentle warming of the depression plate with a micro-burner hastens evaporation of the aqueous solution, leaving the $CoCl_2$ residue in the hollowed-out shot. Heavy electrician's pliers are used to crimp the shot into flattened tablet shape. Final filing and up to 4-5 coats of plastic spray insure a smooth edge to the tag. Measurements of 10 finished tags give a mean single-tag thickness of 1.5 mm and a mean diameter of 7.6 mm. The mean weight of one tag, based on total weight of the ten tags, is 0.5 gm.

Co^{60} is a relatively hot source. At no time should the radioisotope directly contact the experimenter.[2] Forceps should be employed in handling the tags. As standard safety procedure the author carried a pocket dosimeter throughout the course of the project.

Use of a lead bottle for storing and transporting the radioactive tags is recommended. Besides reducing human exposure to gamma rays, the lead shielding helps prevent exposure of film usually carried into the field. Field-tagging technique is relatively simple. An incision one cm long is made parallel to the midline along the dorsum of the toad. With blunt forceps the tag is inserted under the loose skin to a ventrolateral position anterior to the femoral region. No attempt is made to maintain sterile conditions other than to keep the instruments wiped clean, and the incision is not sutured.

[2] See National Bureau of Standards reports on safe handling of radioactive materials.

Dosage Determination

As pointed out by Griffin (1952), the merits of radioactive tagging in any situation must be considered in terms of, first, the maximum permissible radioactivity of the tag, and second, the practical range of detection. Among other factors, considerations of total dosage involve evaluation of the isotope in terms of its half-life. Lachelt (1954) has calculated the optimum half-life to be approximately two-thirds the length of the study. In certain instances, as with game animals, where there might be danger of human contact with the tags, use of a radioelement with a very short half-life may be obligatory. When tagging a montane population of toads, however, the chances of people contacting (much less eating) the animals is extremely remote. The extended half-life of Co^{60} (5.3 years) was deemed advantageous in the present study because theoretically, the toads could be recovered over a period of many years, providing the accumulated radiation dose remained sublethal. The relatively high gamma energy (1.1, 1.3 Mev) of the isotope is necessary for penetrating soil. Ideally, the tag dose should be kept as low as possible, compatible with effective detection, so as to minimize possible behavioral as well as lethal effects. Unfortunately, time was not available in the present study for the laboratory experiments on dosage, behavior, and survival which should precede field experiments.

The tolerance limits of an amphibian exposed to a relatively constant source of radiation are unknown. Under experimental conditions Patt and Swift (1948) determined that single total body exposure of the leopard frog, *Rana pipiens,* to 1000 roentgens of X-ray at 23° C resulted in 81 percent mortality within six weeks. Stearner (1948) reports 50 percent mortality at six weeks for the same species exposed to 700 r. Using the simplified formula presented by Griffin (1952),[3] the author calculated the gamma intensity at the surface of the lead tag. For example, 10 microcuries of Co^{60} emit approximately 25 r/hr at the surface of a platelet-shaped tag 1.5 mm in diameter. The reduction in gamma energy due to lead shielding is only in the order of a few percent. It is apparent that in a matter of weeks at least part of the toad's tissue would suffer exposure to radiation far exceeding the LD_{50} value of 700 r for frogs, if only a few microcuries of Co^{60} were used.

[3] For theory and more precise calculations of internal dosimetry see Marinelli *et al.* (1948), Siri (1949), and Bush (1949).

However, it is well established that the total energy made available by the disintegration of a radioisotope is never completely absorbed by an organ or an entire animal, and a given dose of gamma rays produces less damage when distributed over a long period than when concentrated into a single exposure. Lacking time for further experiments on dosage, the author adopted the principle of using the minimum quantity of isotope which still might prove useful in detection. On this basis, tags of 20-30 microcuries' dose were made for field use.

Detection Methods

At various times during the study two kinds of instruments were available, a Geiger-Müller counter (Tracerlab Su5 Beta Gamma Survey Meter or a Beckman Beta-Gamma Meter) and the much more sensitive Scintillometer (Canadian Aviation Corporation). The former counters were equipped with earphones and three-foot wire leads to the steel-encased counter tubes. Field technique with a Geiger unit involved slowly traversing the study area while dangling the tube about three inches above the surface of the ground. In surveying a gullied stream the tube was moved parallel to the vertical earthern bank where toads at times sought retreat in rodent burrows (Fig. 2). To protect the crystal in the wand of the Scintillometer, the wand itself was usually kept inside the metal case and the instrument used as a single compact unit. By lengthening the carrying strap, it was possible to lower the instrument to near ground level without bending over, an important advantage during long surveying periods.

A more uniform coverage of the study area is possible if one sets up parallel survey lines based on natural features. The distance between these lines theoretically should be twice the effective range of detection, but the choice of a practical working distance must be weighed in terms of tag dose, sensitivity of the instrument, suspected depth of the toads, time available in relation to size of area to be surveyed, and other considerations. With so many variables it is only by experience that one can determine the most efficient plan of survey. The following method of tracking down a source has proved effective under field conditions.

Working along line A paralleling B (Fig. 3), the surveyor should receive maximum tag radioactivity at a point closest to the source (S). In practice, however, due to scattering effects of soil and rock and difficulties in detecting minute changes in radiation level, the operator may determine greatest gamma intensity at point (X).

Fig. 2. Surveying the study area at Tioga Pass with a Geiger-Müller counter. Rodent burrows bordering the small rivulets are retreats favored in summer by the Yosemite toad.

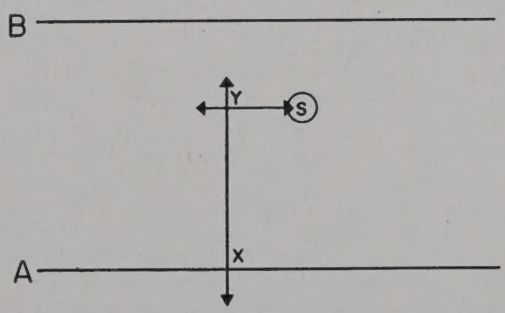

Fig. 3. Diagram illustrating method of tracking down a source (S) of radioactivity from point where it is first detected.

By working at right angles to line A one determines the direction of increased radioactivity. The "right angle only" principle is again followed at point (Y) and repeated as often as necessary until the animal is zeroed in. Field situations may dictate a modification of the above idealized approach. For example, rocky outcrops, fallen logs, banks of streams or ponds, and forested areas

might be situations selected by particular animals. In these places intensive random searching may prove more fruitful than the systematic working of parallel survey lines.

Detection Experiments

The shielding effect of soil is a major limiting factor in the radioactive tagging of subterranean animals, yet the fact that animals can be detected in their underground haunts is the *tour de force* of the method. Godfrey (1954, 1955) had little difficulty in tracing the subterranean positions of small mammals, but these animals seldom excavated to a depth greater than 3 inches. Precise data are lacking, but it is probably reasonable to assume that Yosemite toads may be found at depths exceeding one or two feet (see field data to follow.) To determine how effectively tags of varying dose can be detected with a Scintillometer or a Geiger-Müller counter, a series of simple experiments were conducted under relatively ideal conditions. Co^{60} tags were tested at the surface and to known depths in a moderately compacted loam topsoil. Holding either the Geiger tube or front part of the Scintillometer about 3 inches above the ground, the author took readings at predetermined points along a straight line leading toward the tag source. Time was allowed for the instruments to reach near equilibrium at each point, and a reading was averaged from the range covered by the oscillating meter needle. Secondly, the path was retraced, but this time the surveyor moved steadliy at the approximate rate of one foot per second toward the source. Several such moving runs yielded an average horizontal distance from source M.E.D. (Moving Effective Distance) at which point radiation is sufficiently in excess of background to signal the presence of the tag. It should be pointed out that for the sake of convenience the horizontal distance from source is measured from a point directly above the buried tag. The actual distance from source is the hypotenuse of the right triangle thus formed.

In Figures 4 to 6 the radioactivity is expressed in logarithms of 10^3 milliroentgens per hour, whereas the instrument readings were taken in counts per second (Scintillometer) and counts per minute (Geiger-Müller counter). The conversion factors used were 1800 d/sec and 4000 d/min equal one mr/hr respectively. A high degree of accuracy cannot be claimed for this method of plotting range of detection, but the results are much more useful than theoretical calculations of practical working range.

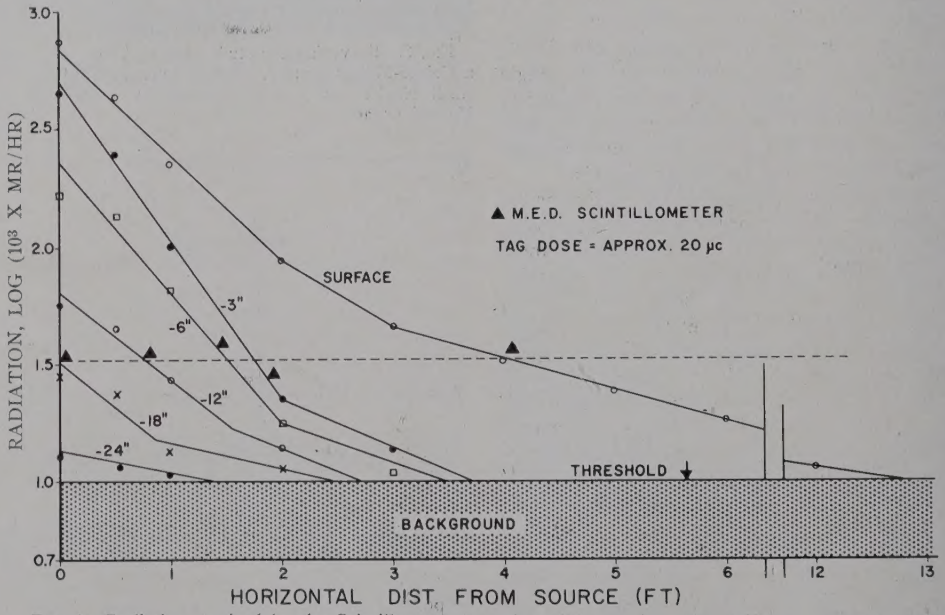

Fig. 4. Radiation received by the Scintillometer at various distances from the Co^{60} tag. Figures accompanying the lines indicate the depths at which the source was buried. M.E.D. (= Moving Effective Distance) is the distance from source where radition was sufficiently in excess of background to be detectable as the instrument was guided slowly toward point zero. The dotted line is the mean radiation value for the combined M.E.D.'s.

Results of tracing a relatively weak tag (approximately 20 μc) with the sensitive Scintillometer are plotted in Figure 4. The practical range of detection (M.E.D.) is approximately 4 feet when the tag lies on the surface of the ground (or if a toad were concealed in the grass). If the source were 12 inches or deeper in the soil, the surveyor would experience difficulty in detecting it. However, the same tag was recovered under field conditions approximately 15 inches below the surface.

The increased effectiveness of detection when tracing a stronger source (approximately 800 μc) is illustrated by Figure 5. The tag on the soil surface can be detected fully 17 feet away with the Scintillometer, and chances of locating the source 2 feet underground are good. The Geiger-Müller counter, though much less sensitive, still can be used effectively in picking up gamma radiation from the same tag buried 18 inches beneath the soil surface (Fig. 6). The greater scatter of the M.E.D. values in Figure 6 reflects the increased difficulty in recording changes in radiation level with the Geiger-Müller counter as compared with the Scintillometer. Correlation of M.E.D. with dosage is summarized in Table I for tags placed on the surface and buried 3 inches. The listed dosage values for all tags are probably slightly higher than actual values due to loss of Co^{60} in pipetting the radioactive solution into the shot and filing of the crimped tag.

TABLE I. Correlation of dosage with effective detection distance

Approximate radio-activity (μc)	Moving Effective Distance (feet)			
	Scintillometer		Geiger-Müller	
	Surface	−3 inches	Surface	−3 inches
20	4.0	1.8	1.9	0.8
40	5.7	2.9	2.3	1.3
60	6.5	3.2	2.7	1.5
500	12.5	4.2	4.6	2.0
800	17.0	5.0	6.5	3.0
2200	19.5	6.5	8.0	3.5
2800	23.0	8.5	9.0	4.6

Field Data

The Yosemite toad habitat chosen for study is part of an extensive mountain meadow at 9900 feet elevation near the northeast entrance to Yosemite National Park. The gently sloping meadow is traversed by numerous low morainal ridges bearing scattered stands of low lodgepole and whitebark pine. Pothole pools and small gullied run-off rivulets meander between the ridges and across open areas dominated by grass and sedge. The study area proper, approximately 100 by 300 yards, is bordered on three sides by ridges 20 to 40 feet high. Shallow breeding pools are present, but most post-breeding toads were found in the wild onion and sedge growth bordering small run-off streams (Fig. 2).

A total of 92 adult and subadult toads was toe-clipped, sexed, and measured in the study area between June 25 and August 30, 1955. Of this total 63 were tagged with tablets containing 20-30 μc of Co^{60}. Detailed data on movements, growth, and other aspects of the ecology of the Yosemite toad will be published separately. The following notes pertain to the usefulness of the method as revealed by field work to date. In evaluating recovery success it must be understood that radioactively tagged toads were sought under varying conditions. During the summer animals were diurnally active to varying degrees, and their retreat sites at night or during the day tended to be close to the meadow surface. By October, on the other hand, surface activity had diminished until toads were not in evidence. Whereas tagged animals were recovered in the summer, two fall surveys failed to yield a hibernating toad. The Scintillometer was not available during the summer months, and use of a Geiger-Müller counter was limited to two surveys. It is probable that recovery success would have been much greater if the highly sensitive Scintillometer had been available.

Twenty-seven toads were Co^{60}-tagged in the study area June 25. Three days later a partial survey was made of approximately ⅕th of the study area. In just over one hour of searching with the single Geiger unit two toads were detected in underground retreats. Radioactivity from one animal was first received at a distance of two feet. By employing the grid method (Fig. 3), the toad was tracked down within a few minutes to its concealed position in a rodent (*Thomomys* and/or *Microtus*) burrow about three inches below the meadow surface.

The following notes illustrate a particular usefulness of the tagging method in gathering and correlating temperature and activity data for these poikilotherms. The cloacal temperature of the toad, 17.6°C, was six degrees higher than the air temperature of the burrow, suggesting that the animal had been active on the surface (air temperature 19.8°C) and sought to conceal itself in the subterranean retreat. The second toad recovered was also traced to a rodent burrow 3 to 4 inches below the surface. This animal was followed as it moved slowly along in the tunnel. Its cloacal temperature coincided with the burrow

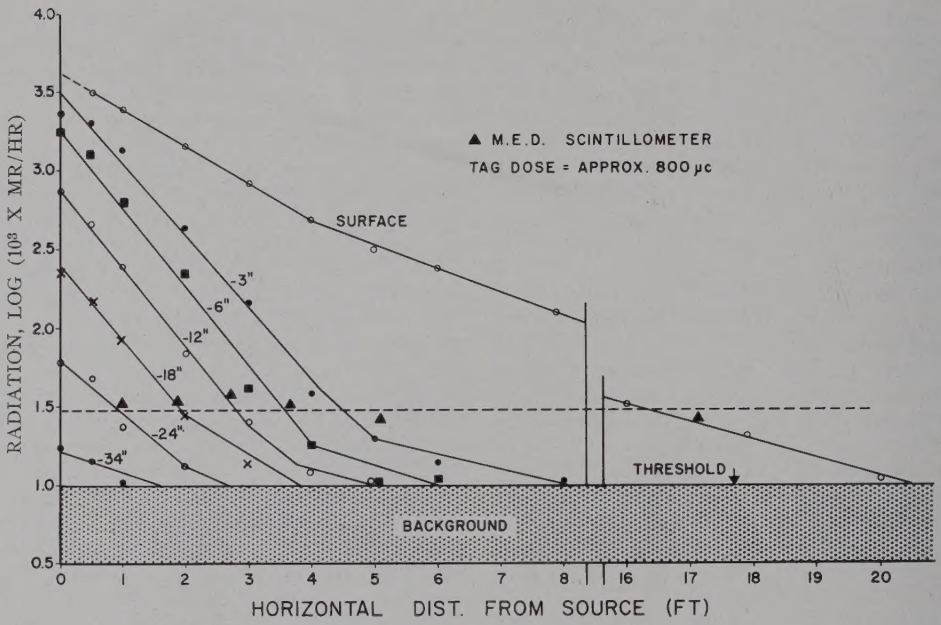

FIG. 5. Same as Fig. 4 but using a stronger tag source, approximately 800 μc.

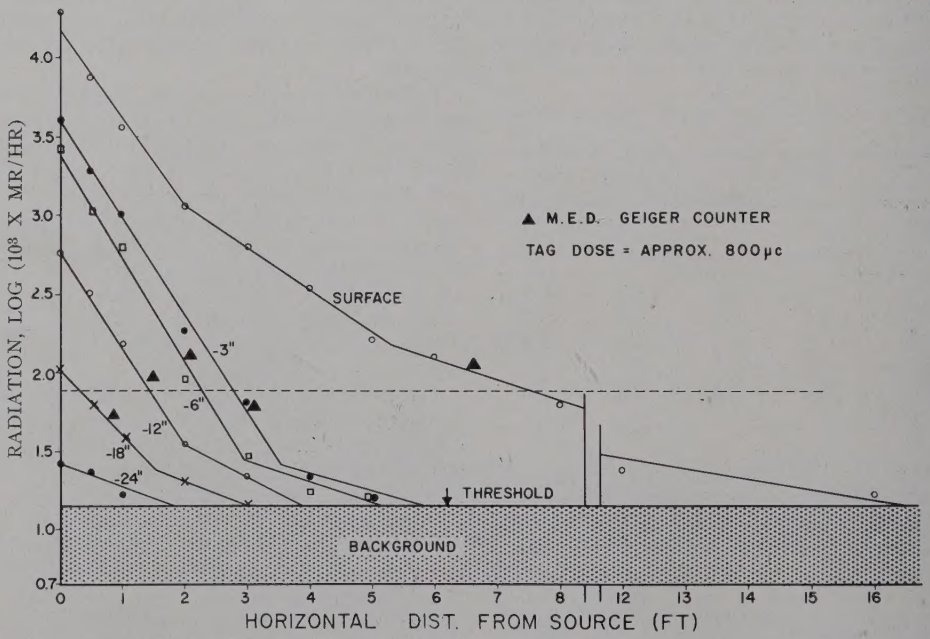

FIG. 6. Same method as Fig. 4 and 5 but based on detection with the less sensitive Geiger-Müller counter.

temperature, indicating that this individual had remained for some time underground. On July 8 an attempt was made to arrive at the study area early in the morning to recover toads in their noctural retreats prior to emergence. Two adults, traced to positions in rodent tunnels before any toads were found active on the surface, had cloacal temperatures of 8.7° and 9.2°C respectively, whereas the air temperature an inch above the ground was 13.8°C. A third cobalt-tagged adult was tracked with the Geiger-Müller counter to a spot in the sedges along a rivulet. Although on the meadow surface, the toad was completely concealed from the surveyor's view.

Two rather intensive surveys, involving the simultaneous use of three instruments (including the Scintillometer), were conducted October 7 and 22, 1955. As mentioned, no hibernating toads were recovered. On October 7 one adult toad, toe-clipped but not tagged with Co^{60}, was found active along a stream bank. During the second fall trip no surface activity was observed, but a single radioactive tag was detected and excavated from a depth of approximately 15 inches in the meadow sod. The recovery of this tag might shed some information on the nature of a hibernation site, although the evidence is circumstantial.

Limited survival data are available, but it is known that tagged toads can overwinter in the field. On July 29, 1956, one year following marking, three toe-clipped adult males were recovered in the study area among several dozen unmarked breeding adults. Two of these animals emitted detectable radiation. The Scintillometer recorded 80 to 90 d/sec four feet from one toad, 30 to 40 counts above background radiation. The cobalt capsule remained lodged beneath the skin in the femoral region, and the animal appeared as active as other males in the area. Although the other animal was definitely "hot," palpation in the field and later laboratory dissection failed to reveal the lead capsule. The incision had healed shut, presumably after the tag had been shed.

The recovered radioactive animals were removed from the population and kept in Berkeley during the summer months. Both died in early September of the same year. That causes other than the radioactivity may have contributed more directly to their death is suggested by the fact that other untagged Yosemite toads collected on the same date died in captivity at approximately the same time.

Discussion

Data gained from simple calculations of total dosage indicate that a toad exposed to a detectable dose may not be expected to survive a long study. For example the use of 20 μc of Co^{60} exposes the animal's tissue to approximately 50 r/hr at the surface of a lead tag 0.15 cm in diameter. To insure survival of the animal for a year or two theoretically would require such a slight dose of radioisotope as to preclude the possibility of effective detection. Field results and dosage-survival experiments, however, suggest that toads continue to live long beyond a predicted survival period.

In preliminary experiments a total of 23 adult toads representing four species of western *Bufo* were tagged subcutaneously with capsules containing from approximately 20 to 2000 microcuries of Co^{60}. In addition, a similar number of control animals, either tagged with dummy capsules or lacking tags, were maintained under similar laboratory conditions. Since the sample is small and mortality was high in both experimental and control groups, the results do not lend themselves to statistical analysis. The significant result is that many of the toads exhibited a high degree of tolerance to strong sources of radiation. Cobalt-tagged animals lived for periods varying from 6 to 41 weeks. An adult female California toad, *Bufo boreas halophilus,* tagged November 7, 1955 with approximately 40 microcuries of Co^{60} was killed September 19, 1956 at the termination of the project. Another adult male of the same species survived 19 weeks exposure to 800 μc. A very hot capsule containing nearly 2000 μc possibly contributed to the relatively early death of two other California toads after periods of 6 and 14 weeks respectively. In most toads the incision through which the tag was inserted healed shut within 3 to 4 weeks, but in the last mentioned cases the incision never knitted properly. Autopsy of all dead tagged toads revealed extensive cutaneous hemorrhage in the vicinity of the capsule. Consistent response of the animals to the foreign object was encasement of the capsule in tough connective tissue about one millimeter in thickness.

Reduced body temperature would undoubtedly favor survival of tagged hibernating toads. Patt and Swift (1948) report 100 percent mortality of *Rana pipiens* in two weeks from exposure to 9000 r single-dose x-radiation, if the frogs were kept at 22°C. However, frogs so radiated but kept at 5°C exhibited 100 percent survival at 4 weeks and 42 percent survival at 6 weeks. The tolerance level for any one species depends upon a myriad of variables including amount of isotope, where and over how long a period it is administered, metabolic state of the animal, etc. Therefore,

theoretical dosage calculations are of limited significance.

Success of the radioactive method in the field demands that the surveyor detect rather subtle alterations in radiation intensity. If the background intensity fluctuates markedly, the emission of gamma rays from the source may be so obscured as to render detection impossible. A prior survey of a proposed study area is highly advisable. Even so, unexpected situations arise. In the present study valuable surveying time has been lost due to fruitless investigation of false leads. Marked increases in radioactivity have been recorded at certain spots in the study area along a small stream course. Careful exacavation of the soil and a repeated testing of soil samples yielded no signs of tags or tagged toads. Instead, high radioactivity, similar to the intensity received from a tag, was traced to approximately a handful of rock and soil material which in one case registered more than 40,000 d/min with the Geiger-Müller counter. The explanation is offered that naturally radioactive isotopes (probably uranium) have leached out of metamorphic rocks at higher elevations and have been deposited in highly localized pockets along a stream. Although such discoveries have intriguing implications for the uranium prospector, they have proved a definite drawback in the search for tagged toads.

The use of radioactive tagging has enabled Godfrey (1954, 1955) to gather data on activity patterns of small mammals to an extent never before realized. *Microtus* and *Talpa* were traced with a high degree of success due primarily to the fact that (1) the tagged animals were active at or close to the surface of the ground, and (2) during the period of the study they did not range laterally over great distances. Apparently for similar reasons the author was able to recover Yosemite toads during the summer. Finding hibernation sites was another matter, since the toads probably withdrew to subterranean retreats below the effective range of detection or dispersed radially out of the study area. The conclusion is that far greater success can be expected if the amphibians or reptiles tagged exhibit limited ranges of vertical and horizontal movement, *e.g.*, some plethodontid salamanders or certain species of lizards.

The theory behind radioactive tracing in biology is well known, but application of radioactive methods to field problems is still largely on a trial-and-error basis. To the researcher contemplating use of the method with amphibians or reptiles the following suggestions are offered.

1. Greater success can be anticipated if the study is of short duration and the dosage can be increased accordingly. Exercise care in choice of an isotope so that it fits your needs in term of energy and half-life (see Griffin 1952).

2. Make a preliminary check of proposed study area to determine difficulties of detection due to irregular background radiation.

3. Determine practical working range for various concentrations of the isotope. By having someone hide a tag in a given area you can simulate a field search for animals in unknown positions.

4. If possible carry out preliminary experiments on dosage and survival. These are necessary for determining the animal's tolerance to the tag as well as to the radioelement. The use of dummy tags which lack the isotope helps to elucidate the effect due to the tag alone.

5. Each tag should be individually identifiable in case it becomes separated from the tagged animal, *e.g.* through predation.

Summary

A method for radioactive tagging of amphibians and its application to field problems is discussed. Tags were made by pipetting known concentrations of Co^{60} solution ($CoCl_2$) into split lead shot. Following evaporation of the aqueous medium the shot were crimped with pliers and the resulting tablets coated with plastic spray. Information on the tolerance of a toad to a constant source of radioactivity is limited. For these field experiments dosage was based on the principle of using the minimum amount of isotope which might prove detectable.

Experimental tracing of radioactive tags with a Geiger-Müller counter and a Scintillometer indicates the effective detection distance correlated with capsule dose and depth to which it is buried. The practical range of detection of a 20-microcurie tag on the soil surface is approximately four feet with the Scintillometer. The same source is detectable if buried to a depth of 12 to 15 inches. A stronger capsule (800 μc) on the surface emits radiation detectable with the Scintillometer from a distance of 17 feet. It can be detected through two feet of soil. The Geiger-Müller counter, although considerably less sensitive than the Scintillometer, is still useful providing the Co^{60} source exceeds approximately 40 μc.

Field technique involves the setting up of parallel survey lines to insure maximum coverage of the study area. An effective method of tracking down a source of radioactivity is described. Part of a population of Yosemite toads, *Bufo canorus* Camp, was marked with cobalt tags of approximately 20 μc each inserted subcutaneously. In summer,

tagged animals were recovered in concealed positions either underground or on the surface. Irregularity of background radiations presented difficulties in surveying the mountain study area. No hibernating toads were recovered during two fall surveys, although a loose capsule was detected and excavated from a depth of 15 inches in the meadow sod. Two radioactive adult male toads were collected one year following tagging. One animal apparently had lost the capsule, whereas the tag remained where placed in the second toad. Both animals were active and normal in appearance, and they survived in the laboratory for an additional three months.

Limited data from dosage-survival experiments in the lab suggest that toads can tolerate much more radioactivity than might be predicted on theoretical grounds. An adult female California toad, *Bufo boreas halophilus,* appeared healthy when killed after 41 weeks exposure to approximately 40 μc of Co^{60}. A very hot source (about 2000 μc) may have contributed to the earlier death of two other California toads at 6 and 14 weeks respectively.

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THE SPRING CAVE-FISH, *CHOLOGASTER PAPILLIFERUS,* IN ILLINOIS

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Introduction

Since Forbes described *Chologaster papilliferus* in 1882, very few data have been published on this amblyopsid. These data are mainly on morphology, taxonomy, evolutionary significance of eye degeneration and distribution of the family Amblyopsidae. Eigenmann (1909) separated the species of the genus *Chologaster* by using the criteria of eye size, body coloration and the degree of development of the sensory papillae. The conclusion was that *C. papilliferus* represents a form which is intermediate between those members of the Amblyopsidae which inhabit surface habitats and those blind members which live in caves.

Forbes and Richardson (1920) mention the habitat and give a species description of *C. papilliferus*. Layne and Thompson (1952) give some distributional data and size measurements. Weise (1953) and Gunning and Lewis (1955) mention the habitat and food of this species. Eigenmann (1909) included some brief behavior observations in his monograph of the cave vertebrates of America. Therefore, the habits, habitat and ecology of this species have been sadly neglected.

ACKNOWLEDGMENTS

During this study the author was aided by many people to whom he wishes to express his deepest gratitude.

The author is especially indebted to Rev. E. J. Long, O. F. M., Quincy College, and to Rev. Robert Brinker, O. F. M., Quincy College, both for assistance in the field, and their many valuable suggestions and criticisms.

For identifications the author is indebted to Dr. Phillip Smith, Illinois Natural History Survey (Crustacea, fish and amphibians); Mrs. G. K. Gloyd, Urbana, Illinois (Odonata); Dr. H. H. Ross, Illinois Natural History Survey (Trichoptera); Dr. Leslie Hubricht, Danville, Virginia (Amphipoda); Dr. J. G. Mackin, Texas A. and M. College (Isopoda); Dr. Libbie H. Hyman, American Museum of Natural History (Turbellaria); and Dr. M. Matteson, University of Illinois (Mollusca).

In addition the author is indebted to students Donald Varner, Patricia Cleary and Daniel Reed for their many hours of laboratory assistance and to Fr. Lawrence Craddock, O.F.M., and to Fr. Victor Hermann, O.F.M., Quincy College, for critically reading the manuscript.

The author is further indebted to Dr. Loren P. Woods, Chicago Natural History Museum, for many valuable suggestions, and to Quincy College for the use of materials during this study.

METHODS AND MATERIALS

Fifteen collections of *Chologaster* have been taken from cold-water springs in Union County, Illinois, during the past four years. Additional collections were not made for fear of population depletion. During an amphipod study (Weise 1953), square-foot samples were taken approximately every two weeks throughout a one-year period from one of the springs by means of a square-foot sampler modified by Dr. W. M. Gersbacher of Southern Illinois University after Welch (1948).

Many living *Chologaster* collections were brought to Quincy College (a distance of 250 miles). These living specimens were transported in jars carried in a tub of ice. None of the specimens was lost in transit.

As a result of the distance separating the author's laboratory from the natural habitat of the fish many natural habitat observations could not be made. In order to compensate for this fact, the author attempted colonization of 36 specimens of *C. papilliferus* in a cold-water cave-spring in Adams County, Illinois, on March 20, 1954. The plant was probably unsuccessful since subsequent observations indicate that the fish are no longer in this spring. It should therefore be noted by persons doing distributional work that these fish could have migrated into subterranean waters connected to those of this region and could reappear in another locality. This seems doubtful however; the probability is that the fish were swept downstream into a connecting stream which empties into the Mississippi River and were taken as food by other fish.

A Winkler method was used for calculating the amount of dissolved oxygen. Standard methods were used for the determination of carbon dioxide and for the determination of methyl-orange alkalinity (expressed in parts per million of calcium carbonate). These methods followed those of the American Public Health Association (1939). The hydrogen-ion concentration was read by using a LaMotte colorimetric set and Hellige discs.

Temperatures and other physical data were recorded.

Specimens were preserved in seventy percent alcohol and are on deposit in the author's laboratory in Quincy College.

Laboratory populations of *C. papilliferus* have been maintained throughout most of this study. These populations ranged in size from 24 to 59 specimens. One population of 23 individuals has lived in laboratory aquaria from May 16, 1953 to the present time, a period of approximately three years. Various sizes of aquaria have been used for this population. With repeated failures in obtaining reproduction, a 10 x 36-inch aquarium was set up with hopes of simulating a cave-spring habitat. About half of the aquarium is inserted into a refrigerator, the door being removed, with the protruding portion resting on a support. The portion of the refrigerator door not closed off by the aquarium has been covered with a one-half inch thickness of wall-board. Artificial aeration is used to create a current of water through a glass tubing lying on the floor of the aquarium. Spring water from local springs, or tap water dechlorinated with Nutra-Chlor, is used in the aquarium. A population of 24 fish has lived in this aquarium for a year. *Gammarus* from local springs is introduced weekly as food.

PHOTOTAXIS AND THIGMOTAXIS

In the laboratory, aquarium populations are afforded areas of retreat under stones placed in the aquaria. The fish use these stones constantly during the daytime. At night the fish are usually found swimming in the open water or resting on the bottom of the aquarium. When the light is turned on during these nocturnal wanderings the

fish will immediately seek concealment under the stones. Removal of these stones and substitution of glass plates permitting the passage of light rays results in the same concealment behavior as when the stones were in place. This behavior occurs even when the stones are placed next to the glass plates. It would seem therefore that the fish, in seeking a retreat, will accept lighted areas as well as darkened areas if there is an object available for a thigmotactic response. If the stones and the glass plates are both removed from the aquarium, the fish will seek out any darkened corner of the aquarium.

Eigenmann (1909) removed the eyes of seven specimens of *C. papilliferus* and observed the same photonegative responses as evidenced before eye removal. This would indicate that the photonegative response of this species is not dependent on an image-perceiving mechanism. Such responses are obviously dependent on some means of orientation. These responses would be dependent on an ability to select areas of concealment by stimuli produced by contact with solid objects or by the stimuli afforded by other factors in the environment, such as currents. The fulfillment of the expression of a photonegative response would therefore be dependent on the highly developed thigmotactic response.

The fish will seek various levels of water depth in order to carry out the touch responses. Cork floats placed in aquaria waters of various depths are used by the fish if no bottom concealment is available. Frequently, four or five fish will gather under a float 2 or 3 inches square. The fish may remain suspended with top anterior portions of the head in contact with the float for an hour or two.

Any disturbance of the water or immediate surroundings, which would cause a vibration of the water, results in an instantaneous response. The fish dart in various directions. If not concealed at the time they will immediately seek a retreat. It is interesting to note that these fish "learn" the habitat to such an extent that very few erratic encounters with objects placed in the aquaria are made. It is also interesting to note that populations which are kept in areas where there is frequent disturbance do not react so violently to the vibratory reactions as those which are kept in more isolated areas.

Both in concealment and in the open the fish will gather in small groups. Whether or not this can be classified as schooling has not yet been determined. The fish, however, will remain in groups, both under observations and at times when there is no disturbance, as is evidenced by the pattern of the feces deposited in the aquaria. Often the deposits will be found in concentrated areas from one to two inches in diameter in open water. While in the grouped position the fish will make many gentle encounters with each other with a resultant positive reaction. Any disturbance of the habitat however will cause violent contact and an immediate "chain reaction dispersal." Likewise free-swimming fish will react positively to gentle touchings of the sides, but with increased pressure an immediate negative reaction is initiated. These reactions may agree with those noted by Allee *et al.* (1949), that in general many animals respond positively to slight local pressures and give a strong negative reaction to more intense ones. It would seem therefore that the grouping of these fish is a thigmotactic response. Breder and Gresser (1941) stated that individuals of the characins which form a retinal image have a strong schooling instinct, whereas those which do not form such an image evidence no such instinct. Individuals with vision tend to rest quietly in a compact school, while the blind continually wander about in an apparently aimless manner Obviously these statements could not be applied to the behavior pattern of *C. papilliferus*.

It might further be noted that thigmotaxis may play an important part in the sex- and species-recognition of this fish. In addition, the absence or rudimentary condition of the pelvics in the Amblyopsidae along with the depressed head and more or less flattened ventral surface could have resulted from natural selection pressure operating to increase the efficiency of thigmotactic responses.

The positive thigmotactic behavior of this species is undoubtedly the most important element of its behavior pattern. The structural basis of this behavior appears to lie in the groups of sensory papillae which are found on most regions of the body and especially concentrated on the head region (Fig. 1). Practically all activities seem to be dependent on this touch mechanism.

Rheotaxis

The rheotactic behavior of this fish is not clearly understood, but appears to be dependent on phototaxis and thigmotaxis. Daytime natural population collections of the fish were successful in areas located beyond the reaches of the current. Night collecting, however, was successful in areas either with or without a current.

During the daytime the fish are found under various objects in the habitat such as stones, sticks, etc. Upon removal of these objects the fish will dart out in search of other concealment areas. During this movement, if they are caught in the

FIG. 1. Photographs of head of *Chologaster papilliferus* showing the distribution and concentrations of the sensory papillae. From Eigenmann (1909).

current, they will respond positively for a short time, exhibiting a fairly strong rheotaxis. This response gives way to a negative response as the fish is forced downstream. In laboratory populations the fish constantly avoid an artificial current during the daytime. Morning examinations of the aquaria, however, frequently reveal feces deposits at the opening of the tube through which the current flows.

These reactions could be important factors in the movements of the fish to and from the subterranean habitat. These nocturnal wanderings into the outside habitat could very easily result in a "trapping" of the fish in this habitat by the sunlight. A better understanding of the subterranean habitat is necessary for further analyses of this behavior.

Temperature Tolerances

The temperatures of the spring-water in the habitat of *C. papilliferus* vary but little. The temperatures range from 54° to 57° F throughout the year.

C. papilliferus has been kept in waters of various temperatures in the laboratory. Most of the culturing was carried on at temperatures ranging from 54° to 64° F.

One group of 24 fish was kept in waters of 43° F for two weeks without adverse effects. Another group of 24 fish was kept in waters of 47° F for two weeks. Ten fish, measuring between 30 and 43 mm, were kept in an aquarium containing water of 82° F for two hours, but were removed after they began to swim nervously around the container in an apparently aimless manner. Five fish of this same group were introduced into waters of 88° F. These fish immediately began to roll convulsively and were promptly removed. No lethal temperature experiments were conducted, but it appears that the upper limit is somewhat near 82° F and that the lower limit is below 43° F.

Populations of *C. papilliferus* have been transferred without tempering from waters of 57° F to waters of 77° F and back to the original waters without any adverse effects and with instantaneous adjustments. This ability to adjust to these conditions is important in the survival of forms which are swept out into swamps or into other surface habitats.

The ability to tolerate such a wide temperature range indicates that *C. papilliferus* is a eurythermic form which inhabits waters frequented by many stenotherms.

Food and Feeding

Thigmotaxis is probably the most important factor in the finding and securing of food in *C. papilliferus*. The author's observations substantiate those of Eigenmann (1909), who makes the following statements concerning the feeding habits:

Chologaster papilliferus detects its food entirely by the sense of touch. Two which were kept in an aquarium for over a year were starved for a few days. They became very nervous continually swimming along the sides of the aquarium. Some individuals of *Asellus* were introduced. These, though quite near, produced no effect if moving in front of *Chologaster*. The moment one came in close proximity to a fish from any direction, by a flash-like motion it was seized. None of them were swallowed. The fishes became very alert after the introduction of the sowbugs and when swimming forward would strike at a part of a leaf if it came in contact with the head of the fish. It seemed evident that the eye gave no information of the character of the object. As the *Asellus* was not altogether to their taste, *Gammarus* was introduced. One of these, swimming rapidly toward the chin of the *Chologaster* from behind and below, was instantly seized when it came in contact with the fish. The eye could not have located the *Gammarus* at all. The action is in very strong contrast to the action of such a fish as *Lepomis*, which detects its food by sight. It is undoubtedly this peculiar method of locating and securing food which has enabled the Amblyopsidae to establish themselves in cave.

Stomach analyses of seventy-five specimens disclosed that only one stomach contained an Asellus. The remaining contents were of the amphipod (*G. troglophilus* Hubricht and Mackin). Gunning and Lewis (1955) record *G. troglophilus*, insects, and detritus from the stomachs of 25 *C. papilliferus*. Since no food utilization studies have been made, it is possible that detritus is carried in with the animal food and is not utilized.

The author has introduced false loosestrife (*Ludwigia palustris* (L.) Ell.), the leafy-liverwort (*Porella pinnata* L.) and watercress (*Nas-*

turtium officinale R. Br.) in aquarium habitats. Artificial lighting was arranged and the plants were kept in the aquaria for two or three weeks. The plants were not eaten but merely used as places of concealment. Two members of the natural community, the isopod (*Asellus brevicauda* Forbes) and the planarian (*Phagocata gracilis gracilis* Haldeman), were introduced also but were not used as food. Tropical fish food likewise remained untouched.

Gammarus was introduced and was instantly seized by the fish. This amphipod from local springs was used as food throughout this study. The gammarid is taken by a vicious sidewise jerking of the head and is immediately swallowed. *C. papilliferus* is a voracious feeder and will take three or four one-half-inch gammarids within a few seconds' time. This type of feeding results in a localized abdominal bulge which forces the viscera medially so that the gammarids show through the translucent skin.

It appears therefore that *C. papilliferus* is basically monophagous and its diet consists mainly of living moving gammarids.

Sexual Differentiation, Gravidity and Breeding

There is no obvious external characteristic for sexual differentiation of immature *C. papilliferus*. Sexual differentiation of mature specimens, *i.e.* above 43 mm in length, however, is fairly easy. The location of the gonads in both sexes is just anterior to the anal fin and can be seen through the translucent body wall. The testis shows through the body wall as a white obliquely convoluted structure (Fig. 2). The single ovary, on the other hand, is an elongated bag-shaped structure which is yellow to yellowish-cream in appearance. This color becomes more of a golden hue in females carrying eggs. Dr. G. E. Mac Ginitie of the Kerckhoff Marine Laboratories used this same method for differentiating sexes in the blind goby (*Typhlogobius californiensis* (Steindachner)). During active feeding the gonads of *C. papilliferus* are forced medially, which makes sexual determination more difficult.

During this study *C. papilliferus* was not seen to reproduce. Maturation of the gametes takes place, but in the female, these are lost, absorbed, or the female dies before reproduction can take place. Two females measuring between 55 and 59 mm in length died after carrying eggs for four months during 1955. Four others of the same size-range lost or absorbed these eggs after carrying them for a similar period of time. At present the author has 15 females ranging in size from 46 to 70 mm which have been carrying eggs since September, a period of approximately 9 months at the time of this writing. These eggs were approximately 0.25 mm in diameter in September and are now approximately 1.5 to 2 mm in diameter and are located about 1 mm posterior to the genital opening.

In gravid females the ovary extends over nearly the whole of the ventral surface (Fig. 3) and the

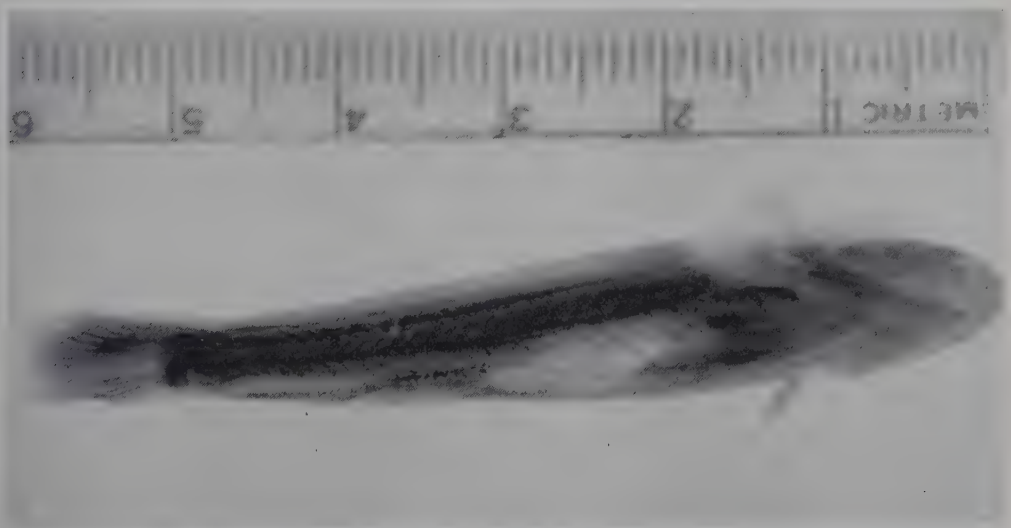

Fig. 2. Ventrolateral view of anesthetized 59-mm male *C. papilliferus*. Testes are the white structures located anterior to the elliptical white spot just in front of the anal fin. Note also the elongate white region from anal to caudal fin. This is probably a fat storage region.

FIG. 3. Living gravid female *C. papilliferus* 55 mm in length. The proximity of eggs to the jugular genital opening can be seen. This female contained 101 eggs of 1.5 to 2.0 mm in diameter. Note the area occupied by the ovary at this time.

eggs can be seen clearly through the body and ovary walls.

Evisceration and examination of the females which had died revealed that the ovary was about 17 mm in length and about 4 to 7 mm in diameter. The ovary of a 55-mm specimen contained 101 eggs, ranging in diameter from 1.5 mm to 2 mm. The ovary was vascularized by a large vessel which ran along the ovary wall and sent branches to individual membranes which enclosed each egg. These eggs were very difficult to remove from the membranes. One 59-mm female contained 95 eggs about 2 mm in diameter.

Three mature males and three gravid females were stripped in an attempt to induce reproduction. The bottle-shaped spermatozoa were introduced with the eggs into a finger-bowl containing water at 15° C. Subsequent examinations, however, disclosed that fertilization had not taken place. The females were 53.3, 60.2 and 61.2 mm in length and contained 80, 202 and 285 eggs respectively. These eggs measured from 1.5 to 2 mm in diameter.

The large size and small number of these eggs indicate that there may be some sort of extended parental care in this species. The forward position of the genital opening in this form may be a breeding adaptation. Eigenmann (1909) found that *Amblyopsis spelaeus* carried the eggs to about the number of 70 in the mouth. These hatched into 5-mm larvae in about a month and the larvae left the mouth when they were approximately 10 mm in length.

Gravid females have been observed in laboratory populations mainly between the months of September and March. Field collections, however, produced gravid females in practically every month of the year with the eggs at various degrees of development. There may be a tendency therefore for the breeding phenomenon of this fish to parallel the tendency of disappearance of periodicity in breeding in cave forms.

Gravid females in the laboratory exhibit no peculiar behavior patterns. No attempt to pair off with males was noted nor were there any attempts at nest building or of isolation.

Breeding in nature is probably carried on in the deeper recesses of the subterranean habitat. During this study ten specimens have been taken or seen which were below 27 mm in length. These specimens were between 10.9 and 14.6 mm. Lewis (1955) found none below 25 mm, and Layne and

Thompson (1952) found none below 23 mm. All but one of these small specimens were collected at night in March 1956, and probably are the smallest on record.

This absence of the smaller size classes in the spring habitat indicates a breeding pattern similar to that of some cave salamanders in which breeding and larval growth take place deep in the caves and are followed by outside migrations.

Ecology

The reported range of *C. papilliferus* is confined to Pope and Union counties in southern Illinois. The reported distribution of this species within the range is very limited. Forbes and Richardson (1920) state that *C. papilliferus* is known only from a cave spring in Union county coming from the foot of a Mississippi River bluff, and from a cave on the Ohio River near Golconda, in Pope County. The author has found the fish in four springs which emerge from the western base of Mississippian limestone bluffs in the Pine Hills region of Union County. Further distributional studies in southern Illinois will probably reveal new localites in which the fish are found.

The western base of the limestone bluffs in Union County represents the eastern extension of the Mississippi River bottomlands in this locality. The Pine Hills region is located at the southern limit of Illinoian glaciation.

Several cold-water springs flow westward from the base of the bluffs and empty directly, or with intervening spring-streams, into the Pine Hills Swamp. On occasion, two to seven *C. papilliferus* have been found in three of these springs, while as many as 100 have been found periodically in a fourth spring and its stream. This spring, along with its spring-stream, is the habitat under consideration. The location of this spring, spring-stream and the Pine Hills Swamp is approximately one mile east of LaRue, Illinois.

The waters of this spring flow from the base of the limestone bluff into a sunken upright sewer culvert approximately 15 in. in diameter. Median openings in the sides of the culvert permit water to flow through the culvert and maintain a pool of water approximately 15 in. in depth within the culvert. The spring-stream proper extends from this culvert to its termination in the swamp, a distance of approximately 100 yards. A stream bed consisting mainly of rock and sand is found throughout the first 25 yards of this distance. This bottom type rather abrupty blends into one of bottomland mud and silt. This latter condition is prevalent throughout the remaining 75 yards of the spring-stream.

The width of the stream varies from about 3 feet throughout the first 10 to 15 yards to about 1 foot for the remainder of its length. The configuration of the bottom is fairly level save for a slight uparching about 15 yards downstream from headwaters and a gentle slope of from 3 to 5 inches following this uparching.

The depth of the water is usually from 1 to 3 inches in the rock-sand region of the stream and from 1 to 5 inches in the mud-silt region. This greater depth in the latter region is caused by temporary flooding of the area during late spring and early summer when the backwaters of the swamp extend out over the region.

The volume output and current velocity were not measured but appeared to reach their maximum during the late spring and early summer.

Temperatures of the waters of the rock-sand region ranged from 54° to 57° F throughout the year. The temperatures of the waters of the mud-silt region were checked periodically and were found to range about 2° above those of the waters of the rock-sand region. This stability is caused in part by the shading effect of the bluffs.

Extensive chemical sampling was not undertaken. Twelve analyses were made of the waters of the rock-sand region between January 21, 1951 and August 11, 1952. The dissolved oxygen ranged from 7.3 to 11.8 mg/l. The free carbon dioxide content varied from 6.0 to 13.3 mg/l, whereas the methyl-orange alkalinity as expressed in mg/l of calcium carbonate ranged from 75.0 to 150.0. The pH remained constant at 6.8 in this region. Two other springs containing *C. papilliferus* also had constant readings of 6.8. Laboratory populations, however, show no adverse effects from waters with a pH of 8.0.

The vegetation of the rock-sand region consisted mainly of a large bed of watercress (*Nasturtium officinale* R. Br.). This bed extended from about 5 yards of headwaters downstream for approximately 10 yards and occupied most of the width of the stream bed. Another small bed of this plant was located at the junction of the rock-sand region with the mud-silt region.

The vegetation of the mud-silt region consisted of the roots and leaves of plants lining the stream bank and of floating swamp forms which were carried into this region by the backwaters of the swamp. The grass (*Panicum* sp.), the bulrush (*Scirpus* sp.) and the sweetflag (*Acorus calamus* L.) comprised the major species of the rooted forms. The floating swamp forms were the duckweeds (*Spirodela polyrhiza* (L.) Schleid., *Wolffia columbiana* Karst, *Lemna minor* L., *Lemna tri-*

sulca L.) and the mosquito fern (*Azolla mexicana* Presl.).

The spring-stream species composition and distribution indicated that two rather well defined communities were present, a rapids and a pool community (see Table I).

TABLE I. SPECIES COMPOSITION OF THE RAPIDS COMMUNITY

Spring cave-fish (*Chologaster papilliferus* Forbes)
Amphipod (*Gammarus troglophilus* Hubricht and Mackin)
Ostracod (*Cypris* sp.)
Water mite (*Megapus* sp.)
Planarian (*Phagocata gracilis gracilis* Haldeman)
Caddisfly (*Pyenopsyche* sp.)
Isopod (*Asellus brevicauda* Forbes)
Snail (*Physa gyrina* Say)
Snail (*Ventridens demissus* Binney)
Green frog (*Rana clamitans* Latreille)
Cricket frog (*Acris blanchardi* Harper)
Leopard frog (*Rana pipiens sphenocephala* Cope)
Long-tailed salamander (*Eurycea longicauda* (Green))
Cave-salamander (*Eurycea lucifuga* (Raf.))
Crayfish (*Cambarus diogenes* Girard)
Midge larvae (*Tendipes* sp.)
Unidentified Diptera and Coleoptera.

SPECIES COMPOSITION OF THE POOL COMMUNITY

Green sunfish (*Lepomis cyanellus* Rafinesque)
Western lake chubsucker (*Erimyzon sucetta kennerlii* Girard))
Minnow (*Notropis* sp.)
Round sunfish (*Centrarchus macropterus* Lacépède)
Swamp darter (*Etheostoma gracile* (Girard))
Pirate perch (*Aphredoderus sayanus* (LeSueur))
Mudminnow (*Umbra limi* Kirtland)
Starhead topminnow (*Fundulus dispar* (Agassiz))
Mud pickerel (*Esox vermiculatus* LeSueur)
Black crappie (*Pomoxis nigro-maculatus* (LeSueur))
Brown bullhead (*Ameiurus nebulosus* (LeSueur))
Mosquito fish (*Gambusia affinis* (Baird and Girard))
Pigmy sunfish (*Elassoma zonatum* Jordan)
Bluegill, (*Lepomis macrochirus* Rafinesque)
Caddisfly (*Pycnopsyche* sp.)
Dragonfly *Libellula incesta* Hagen)
Dragonfly (*Libellula vibrans* Fabricius)
Crayfish (*Cambarus diogenes* Girard)
Black-striped top minnow (*Fundulus notatus* (Rafinesque))
Cricket frog (*Acris gryllus blanchardi* Harper)
Leopard frog (*Rana pipiens sphenocephala* (Cope))
Green frog (*Rana clamitans* Latreille)
Water scavenger beetle (*Hydrophilus triangularis* Say)
Water bug (*Belostoma* sp.)
Predacious diving beetle (*Dytiscus* sp.)
Aquatic anelid (*Lumbriculus* sp.)
Snail (*Helisoma* sp.)
Unidentified insects and dipterous larvae.

The numbers of species in the rapids community was much smaller than that of the pool community. Odum (1954) states that spring communities are characterized by relatively small numbers of species and that the more stable conditions seem to provide fewer ecological niches. An occasional crayfish (*Cambarus diogenes* (Girard)), a few caddisflies (*Pycnopsyche* sp.) and a larger number of ostracods (*Cypris* sp.) were collected from the pool community but were found in much larger numbers in the rapids community. The frogs (*Rana clamitans* Latreille, *Rana pipiens sphenocephala* Cope and *Acris gryllus blanchardi* Harper) were frequently found in both communities. *C. papilliferus* was found only in the rapids community under rocks or other objects during the daytime and swimming in open water at night.

The population density of the vertebrates of the rapids community was difficult to ascertain. These forms were very difficult to capture in a square foot sampling device and the many places affording areas of concealment made the taking of an accurate census practically impossible. A census of the cave fish was attempted on several occasions and revealed an important fact. On January 23, 1954, only 25 cave-fish could be found in the spring-stream. However, on April 14, 1954, the number of fish had increased to 104. The size classes on the last collection date prohibited a consideration of reproduction as the cause of this increase. Gunning and Lewis (1955) noted this same trend. Night sampling by these authors and by the present writer revealed that the fish wil move into the subterranean habitat periodically during the daytime and out into the surface habitat at night. On November 4, 1955, the author found only 3 fish in this spring and 1 fish in another spring during daytime sampling. That night the fish could be seen coming from their subterranean habitat. Twenty-seven fish were taken during this collecting period. Obviously, this behavior would further complicate the taking of an accurate census. Consequently, the vertebrates are not included in the population density analyses.

The perennial and incidental invertebrates of the rapids community, along with their densities and alcohol-volume displacements, are shown in Table II. Obviously, *G. troglophilus* is the most abundant member of the community. The lowest population level of this form was found on April 22, 1952. At this time the number of individuals per square foot was 43 and the alcohol displaced by these individuals was 1.7 cc. The percentage of species composition made up by *Gammarus* at this time was 13.2. The population peak occurred on December 21, 1951. At this time 718 gammarids were found per square foot. This sample showed a volume displacement of 5.9 cc and a percentage species composition of 82.7. Although there is no datum to show correlation between the numbers of *Gammarus* and *Chologaster* present at any one time, this information is im-

TABLE II. Population density of perennial and incidental invertebrates in the rapids community, per square foot

Date	Asellus	Cypris	Megapus	Phagocata	Gammarus	Incid.	Total
26 Oct. 1951	2	296	52	10	399	18	777
19 Nov. 1951	7	16	38	42	428	18	549
11 Dec. 1951	4	208	50	66	563	11	902
21 Dec. 1951	5	90	36	3	718	16	868
8 Jan. 1952	0	9	44	166	555	41	815
21 Jan. 1952	0	89	11	5	276	15	396
7 Feb. 1952	10	35	25	21	458	14	563
22 Feb. 1952	4	32	20	121	440	35	652
15 Mar. 1952	2	0	12	50	220	7	291
30 Mar. 1952	6	8	47	11	394	16	482
22 Apr. 1952	1	261	7	5	43	7	324
16 May 1952	0	244	53	4	141	29	471
9 June 1952	5	25	19	20	150	15	234
21 June 1952	0	118	88	4	321	15	456
5 July 1952	11	2	2	69	408	11	503
20 July 1952	15	35	16	59	362	42	529
11 Aug. 1952	10	6	2	44	175	21	258
2 Oct. 1952	2	25	3	76	269	18	393
18 Oct. 1952	0	9	15	70	258	4	356

Volume displacements of Gammarus and other invertebrates in cc, and the percentage composition of Gammarus (by number)

Date	Vol. Disp. Gammarus	Vol. Disp. All others	Percent Gammarus (by no.)
26 Oct. 1951	8.5	1.0	51.3
19 Nov. 1951	5.1	.6	78.9
11 Dec. 1951	3.5	.5	62.4
21 Dec. 1951	5.9	.8	82.7
8 Jan. 1952	6.4	.8	68.1
21 Jan. 1952	5.0	.8	69.7
7 Feb. 1952	4.0	.8	81.3
22 Feb. 1952	5.9	.9	67.5
15 Mar. 1952	2.5	.9	75.6
30 Mar. 1952	5.8	.4	81.7
22 Apr. 1952	1.7	.1	13.2
16 May 1952	1.5	.4	33.5
9 June 1952	2.5	.4	64.1
21 June 1952	5.5	.1	50.6
5 July 1952	7.5	.2	81.1
20 July 1952	11.8	1.2	68.4
11 Aug. 1952	6.7	.9	67.8
2 Oct. 1952	8.0	.4	68.4
18 Oct. 1952	5.8	.5	72.4

portant from the standpoint of food available to *C. papilliferus*.

Lagler (1952) states that a volume displacement above 2 cc per square foot and numbers above 50 per square foot would indicate a food grade of exceptional richness. Since this gammarid constitutes nearly 100% of the diet of *C. papilliferus* it can be seen that the availability of food for this fish is very high.

Only a few frogs and salamanders were available for dissection. Their stomach contents consisted of the water mite (*Megapus* sp.), the amphipod (*G. troglophilus*), the isopod (*A. brevicauda*) and several terrestrial arthropods. The large size and the habits of the vertebrates more or less eliminate a consideration of active predation by other members of this community. On one occasion in the laboratory, however, a population of 10 cavefish was kept in an 8 x 10-inch aquarium along with approximately 150 gammarids. Six amphipods measuring about ½ inch in length had seized a fish by the caudal fin. The fish was "held down" while the gammarids consumed about half of the fin. The fish measured 30 mm in length. It would seem, therefore, that the smaller size classes of *C. papilliferus* could fall prey to large numbers of amphipods. It would appear in addition that at least the larger fish are relatively free from active predation pressure exerted by other members of the rapids community. No doubt birds and reptiles take a few of the specimens but the nocturnal habits of the fish tend to limit this action.

At times high waters of the swamp would extend out over the mud-silt region of the stream. This condition would permit movements of the pool and swamp species into the rock-sand region. Both the spring-stream and the region of the swamp at the spring-stream entrance were seined during these times. A star-head topminnow (*F. dispar*) and a mud-minnow (*U. limi*) were found in association with *C. papilliferus* during high water periods. Stomach analyses of these forms and of the green sunfish (*L. cyanellus*), the round sunfish (*C. macropterus*), the pirate perch (*A. sayanus*), the mud pickerel (*E. vermiculatus*), the bluegill (*L. machrochirus*) and of the brown bullhead (*A. nebulosus*) revealed that these forms had not taken *C. papilliferus*. The author has found *C. papilliferus* in association with the green sunfish and the mud minnow in beds of the leafy liverwort (*Porella pinnata* L.) and the false loose-strife (*Ludwigia palustris* (L.) Ell.) in other spring communities. In all cases, however, Gammarus was present. Gunning and Lewis (1955) found the cave fish in association with these and other fish in a green alga-yellow pond-lily duckweed community of the swamp. These authors found that the stomach contents of two mud minnows, collected from the spring-stream under consideration, each contained a cave fish.

The spring habitat of *C. papilliferus* offers many advantages for habitation by this form and for spring stream species in general: the relative stability of physical and chemical factors, a rocky bottom affording many areas for concealment, a relatively low predation pressure, a high degree of food availability, and an underground retreat for breeding or escape from adverse factors.

Conclusions

C. papilliferus exhibits a highly developed photonegative response. However, thigmotaxis is undoubtedly the most important element of the behavior pattern of this fish. Practically all activities seem to be dependent on this touch mechanism. The structural basis of thigmotaxis appears to lie in the sensory papillae which are located on various parts of the body and especially concentrated on the head.

The rheotactic responses of this fish are not clearly understood but appear to be reliant on phototaxis and thigmotaxis.

The temperature of the water in the natural habitat ranges from 54° to 57° F throughout the year. Laboratory populations of *Chologaster* have been kept in waters with temperatures ranging from 43° to 77° F without apparent adverse effects. This wide temperature toleration indicates that *Chologaster* is a eurythermic form which lives in a habitat occupied by many stenotherms. This wide range of temperature tolerance is important in the survival of a species swept from cold underground waters into warm surface waters.

Gammarus is found in large numbers in the habitat of *Chologaster* and furnishes nearly 100% of the food of this fish. The taking of food by this fish is dependent on thigmotaxis.

Sexual differentiation of matures, *i.e.,* above 43 mm in length, is accomplished by noting the color of the gonads through the body wall; females have yellow gonads and males have white gonads.

The females carry eggs of from 1.5 to 2.0 mm in diameter for long periods of time in laboratory populations. Reproduction has not been observed. In nature reproduction probably occurs in the deeper recesses of the subterranean habitat.

C. papilliferus is found in typical cold spring waters in Pope and Union counties in southern Illinois. This fish is found under rocks and other objects during the daytime but is usually found moving in the open waters at night. These nocturnal movements carry the animal to and from the connecting subterranean habitat.

This fish is found in association with several typical spring inhabitants. Its most important associate however is *Gammarus* with which it has always been found. Large numbers of a small number of species are found in association with *Chologaster* but very little predation pressure is exerted on this fish by these associates.

The habitat of *Chologaster* offers many advantages including stable physical and chemical conditions, large amounts of food, relatively low predation pressure, and an underground retreat for escape from adverse factors and probably for breeding.

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AN ANALYSIS OF POST-WISCONSIN BIOGEOGRAPHY OF THE PRAIRIE PENINSULA REGION BASED ON DISTRIBUTIONAL PHENOMENA AMONG TERRESTRIAL VERTEBRATE POPULATIONS

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During recent years a mass of distributional data has been assembled as ranges of many animals in eastern North America have become known in greater detail. As our knowledge increased, evidence has accumulated to suggest that biogeographic events of the postglacial period played a significant role in determining present distributional patterns. Since this evidence permits generalizations remarkably parallel to inferences drawn from other biogeographic data, the time is at hand for a summary of the distributional information and an attempt to correlate data from the several sources. As a working hypothesis, a reconstruction is offered of the probable steps involved in producing the present distributional complexity of the midwestern and northeastern United States. In a broadly inclusive sense, this geographic area is the Prairie Peninsula region.

I have profited by discussing this subject with a number of zoologists; the great number of these contributors prevents mentioning each one by name. I have drawn freely from published accounts without citing the sources of information in every case. The distributional maps, for the most part, have been constructed by consulting a number of published studies, and my interpretations are not necessarily those of the authors of these studies. I am indebted to my associates Drs. C. W. Collinson, J. C. Frye, H. B. Mills, H. H. Ross, K. P. Schmidt, R. B. Selander, H. M. Smith, L. J. Stannard, and H. B. Willman for reading all or parts of my manuscript and to Dr. S. A. Minton and Roger Conant for calling my attention to certain illustrative distributional patterns.

The highly complex patterns of present animal distribution reflect the availability of suitable habitat (*sensu lato*), the operation of such broad limiting factors as temperature and humidity, the faunal history of the region, the amount of human disturbance, and various combinations of these factors. Accordingly, attempts to reconstruct dispersals of animals are speculative, and a synthesis built on a limited amount of evidence is necessarily sketchy and diagrammatic. Considerable revision of certain assumptions and modification of several of the illustrative examples will doubtlessly be necessary. Nevertheless, a general picture emerges from the data available that is in essential agreement with present concepts of postglacial biogeography. This picture is greatly simplified in the present case by three conditions.

First, the terrestrial vertebrates (amphibians, reptiles, and small mammals) are among the most reliable zoogeographic indicators because (a) their inability to fly and large size reduce the probability of transport by wind, (b) they are terrestrial and accordingly not likely to have their ranges altered by floods and the process of stream capture, (c) they are more or less chained to a specific type of habitat and not sufficiently motile to cross moderate-sized barriers of unsuitable habitat, (d) they tend to have relatively small home ranges, and (e) they have been studied in enough detail in eastern North America for their taxonomy and distribution to be comparatively well known.

Second, the synthesis presented herein is based almost entirely on interpretations of relict populations and of trends in geographic variation, the two most indicative and lucid of distributional phenomena. When apparently relict populations exist some distance from the main segment of range of a species, it is assumed that either (a) the species is actively colonizing new areas at the present time or (b) the range of the species once encompassed the site of the relict but has since become disjunct. For reasons outlined in the preceding paragraph, saltatorial colonization of new areas by terrestrial vertebrates under natural conditions is deemed unlikely. However, animals are transported by man, and it is conceivable that a gravid female or a pair of waifs so transported could initiate a new colony in a suitable habitat well removed from the natural range of the species. Among the more obvious means by which this sort of colonization might occur are the deliberate release of individuals, the escape of pets, and the inadvertent transport of animals in shipments of materials or in balled roots of trees and shrubs.

Even if these considerations can be ruled out, some caution is still advisable in interpreting relicts because of the possibility that the specimens on which records are based may bear erroneous locality data or may be misidentifications. Even when a population is known to exist as a relict, there is a chance that it is isolated because human activity has been responsible for the destruction

of favorable habitat within the hiatus. Despite these difficulties in determining true relicts, the evidence indicates that they do occur and are, in fact, rather numerous within the Prairie Peninsula.

Third, approximately half of the area under consideration was buried under ice during the Wisconsin glacial maximum, and it is a virtual certainty that the glaciated region was then uninhabited by terrestrial vertebrates. Since the retreat of the ice front, these animals have re-entered the glaciated region. Concerning ourselves only with the repopulation of the greater part of the Prairie Peninsula region by our present fauna, we need go no further back in time than the Wisconsin glacial maximum.

Postglacial Biogeography in Eastern North America

Postulated climatic phases

There has been considerable disagreement as to the sequence and length of the post-Pleistocene climatic phases since Blytt, Sernander, and others in the late 19th Century first attempted to describe these changes in climate. Despite the disagreements and diversity of chronologies, however, general agreement on a cool-warm-cool sequence prevails. Much of the pioneer work was done in Europe and has been summarized by Zeuner (1946). Excellent summaries of the biogeographic investigations in North America are given by Flint (1947) and Deevey (1949). The impetus afforded this field of research by pollen studies since 1930 and by radiocarbon studies since 1950 has resulted in several symposia within the past few years. These studies have contributed to an understanding of postglacial climates and at the same time prompted students of plant and animal distribution to re-examine their data.

The contribution of pollen profiles

Currently, the postglacial chronology for eastern North America does not appear to be a subject of great controversy, and radiocarbon techniques have provided definite dating for some of the climatic phases (Zumberge and Potzger 1955). A chronology, based on pollen profiles, is presented by Deevey (1949, p. 1356). In brief, the sequence is as follows:

After the retreat of the ice front, a tundra flora presumably moved northward, parallel to the glacial front, although positive evidence in the way of tundra pollen is available only from Maine. The tundra was succeeded by spruce and fir forest, and it is inferred that the climate was still cool. Subsequently, a predominance of pine pollen appeared, suggesting a warmer and possibly drier period. The next period was characterized by abundant pollen of oak and such mesophytes as beech, hemlock, and elm, indicating a still warmer but probably more humid phase. This phase was followed by the Xerothermic period with a predominance of oak and hickory pollen, suggesting aridity and high temperatures. It is presumed that an eastward invasion of grassland occurred or at least that a steppe vegetation became more extensive than at present, although pollen of a steppe vegetation is apparently lacking in the profiles. After the Xerothermic period, the climate apparently became cooler and wetter as it is today. The recent Indiana and Illinois pollen deposits are still predominantly oak-hickory, but the areas to the north (Minnesota and Wisconsin) and to the east (Ohio and New England) show the oak-hickory deposit overlain by pollen of mesic forest trees of the same species which occur in these areas at present.

The duration of the Climatic Optimum or Thermal Maximum of geologists is uncertain. It may have extended from the warm, dry pine phase through the oak-mesophyte and Xerothermic phases. As used herein, Climatic Optimum is synonymous with the oak-mesophyte (warm, moist) phase. There are several minor conflicts between the North American and European records, but the general chronology is similar on the two continents. The steppe invasion from west to east in North America had a mirror image in Eurasia.

Evidence from distributional patterns

The significance of distributional data was clearly recognized by Adams (1905), Gleason (1920), and others. Data to support phytogeographical shifts corresponding to the postulated climatic phases have been presented by such investigators as Transeau (1935) and Sears (1942). Various authors have employed glacial and postglacial faunal migrations to account for specific ranges, and the occurrence of so-called Ice Age mammals such as the woolly mammoth and walrus in southern areas is well documented. One of the first zoologists to analyze the distribution of a number of animals in the light of postglacial changes was K. P. Schmidt (1938), who pointed out that many reptilian ranges indicate an early postglacial immigration into the east from the Great Plains. Schmidt's contribution, which was concerned almost entirely with the grassland fauna, is stimulating and significant, although some of his conclusions are at variance with biogeographical evidence now available. He visualized a belt of grassland directly succeeding the tundra and paralleling the retreating ice front, and he

postulated that this belt of steppe was the corridor connecting the Great Plains with eastern North America. Thomas (Conant, Thomas, and Rausch 1945) has suggested that Schmidt's data support equally well the hypothetical eastward dispersal of western organisms during a Xerothermic phase and that postulation of a corridor immediately after the glacial retreat was unnecessary. Thomas (1951) analyzed the distribution of the Ohio fauna and presented a wealth of new distributional information. Dillon (1956) has recently discussed the climate and life zones of the entire continent during Wisconsin glaciation and has presented new data and ideas as well as an excellent summary of glacial investigations.

Reconstruction of Faunal History

Beginning with the Wisconsin glacial maximum, we can be assured that the pre-existing fauna was entirely erased within the area covered by ice (Fig. 1). South of the ice front there can be little doubt that the fauna was different from that of today, but its nature is wholly conjectural. Among current students the extremes in viewpoints are represented on the one hand by Braun (1951) and Thomas (1951) and on the other by Deevey (1949). Dr. Braun and her associates hold that there is abundant evidence to indicate little biological displacement in southern United States during glacial maxima of the Pleistocene and that pre-Pleistocene and Pleistocene events are implicated in a consideration of present distributional patterns. Deevey and his followers, however, believe the presence of spruce pollen in Louisiana and Texas bog samples demonstrates that a pronounced chilling influence extended as far south as the Gulf Coast and that postglacial events have been sufficiently profound to overshadow the earlier effects and account for the present biogeographic complexities.

Post-glacial-maximum pre-Climatic-Optimum (pine) phase

No definite evidence is contributed by the distributional patterns of terrestrial vertebrates, and a compromise on the extent of biological displacement seems advisable. This intermediate viewpoint recognizes that the fauna of the glaciated territory was forced southward or eliminated but does not imply that the boreal fauna completely replaced a more southern faunal type or that the area south of the ice front was appreciably colder than at present. This view holds that an admixture of ecologically segregated boreal and austral elements existed, possibly almost side by side, near the ice front but within unglaciated territory. This seeming hodge-podge of biota would actually be expected since the retreating ice front must have fluctuated considerably for many years. The series of recurring advances and recessions of ice and the quantity of water poured onto the landscape by the melting ice probably complicated the environment of the glacial border to a great extent.

Some indication of the distance that the northerly animals penetrated southward into unglaciated territory is furnished by the known boreal relicts still existing today (Fig. 1). Three species of amphibians with a predominantly northern distribution now have the main segment of their ranges within the area covered by the Wisconsin ice sheet and have scattered relicts in unglaciated territory. The eastern four-toed or bog salamander, *Hemidactylium scutatum* (Fig. 2), is definitely known to occur as a relict in Georgia, northern Alabama, and, if an old published record is trustworthy, at Hot Springs, Arkansas. Although evidence from the wood frog, *Rana sylvatica* (Fig. 3), is complicated by the existence of one subspecies behaving as an eastern and of another, as a northern form, relict populations of one or the other occur to the south in northern Arkansas, central Kansas, and northern Colorado. The red-backed salamander, *Plethodon cinereus* (Fig. 4), also has a disjunct range, although this fact has not previously been pointed out. An Ozark Uplift segment of the range is separated from the main range in eastern North America by a hiatus of 100 miles. The range of the bog turtle, *Clemmys muhlenbergi* (Fig. 5), also illustrates a more widespread range in former times. This rare turtle now appears to consist of four separate colonies, and one of these is located well to the south of the other three. It can be concluded that the influence of a fauna, now regarded as distinctly northern, once extended as far south as Georgia and Arkansas, and the most probable time for this to have occurred is clearly at the height of the glacial maximum.

The distributional patterns of three other northern species with southern relict populations are less dramatic but worth mentioning. Butler's garter snake, *Thamnophis butleri* (Fig. 6), and Kirtland's water snake, *Natrix kirtlandi* (Fig. 7), are both endemic to the Prairie Peninsula. They have been regarded as Xerothermic relicts by Schmidt (1938) and Conant (1943), who visualize them as immigrants from the west which persisted in the Prairie Peninsula following the Xerothermic period but were eliminated elsewhere. They are considered glacial relicts by Thomas (1951) who suggests that these snakes

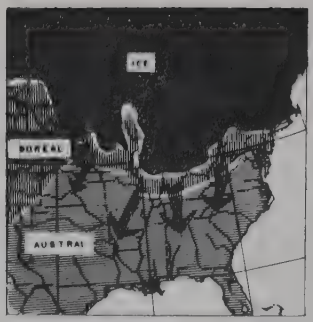

FIG. 1. WISCONSIN GLACIAL MAXIMUM.

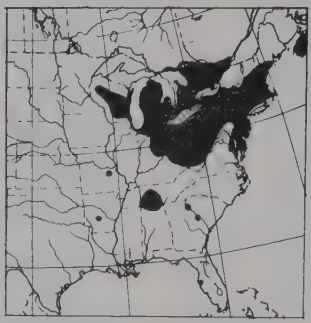

FIG. 2. RANGE OF HEMIDACTYLIUM SCUTATUM.

FIG. 3. RANGE OF RANA SYLVATICA.

FIG. 4. RANGE OF PLETHODON CINEREUS.

FIG. 5. RANGE OF CLEMMYS MUHLENBERGI.

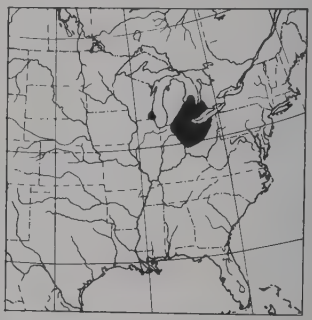

FIG. 6. RANGE OF THAMNOPHIS BUTLERI.

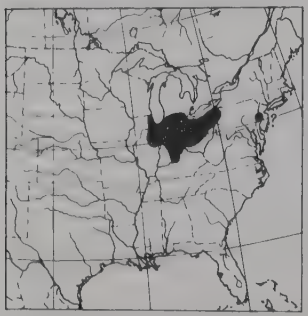

FIG. 7. RANGE OF NATRIX KIRTLANDI.

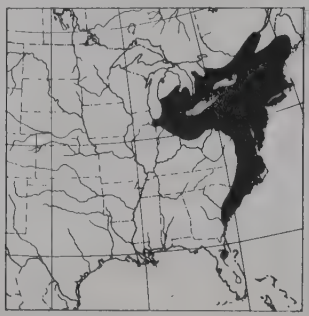

FIG. 8. RANGE OF CLEMMYS GUTTATA.

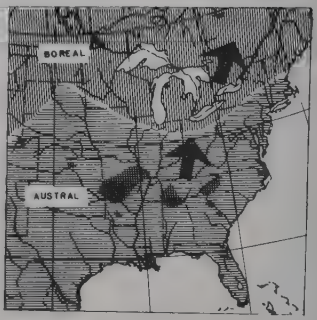

FIG. 9. RETREAT OF ICE SHEET.

probably survived the glacial advance somewhere close to the ice front and re-entered glaciated territory following the retreat of the ice. The spotted turtle, *Clemmys guttata* (Fig. 8), occurs farther to the south on the East Coast than the preceding examples and thus appears to be less distinctly boreal. If an old published record for the species in Marion County, Florida, is valid, however, it would appear that this turtle once had a more southern range than at present. It should be noted that southeastern herpetologists generally discount this record in the absence of recent collections of the spotted turtle in Florida.

It can be reasoned that as the moderating climatic conditions advanced northward over the recently glaciated landscape, immigration of animals was contingent upon the availability of suitable habitat and the proximity of populations which could recolonize the new areas. It can be inferred that those animals occurring nearest the glacial border were the first to re-enter the unoccupied region (Fig. 9). The composition of the fauna during the tundra and spruce-fir stages is totally unknown, but it is probable that the amphibian and reptilian faunas were quite impoverished inasmuch as these ecological associations are notoriously poor in these groups today. It is reasonable to believe that boreal animals were

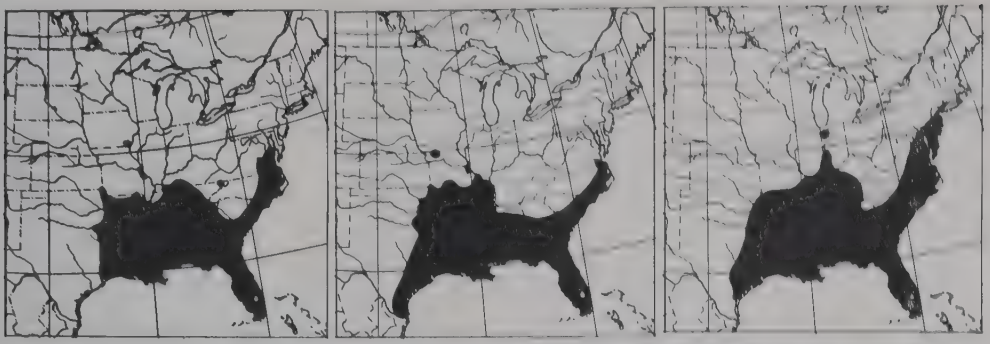

FIG. 10. RANGE OF MICROHYLA CAROLINENSIS. FIG. 11. RANGE OF AGKISTRODON PISCIVORUS. FIG. 12. RANGE OF KINOSTERNON SUBRUBRUM.

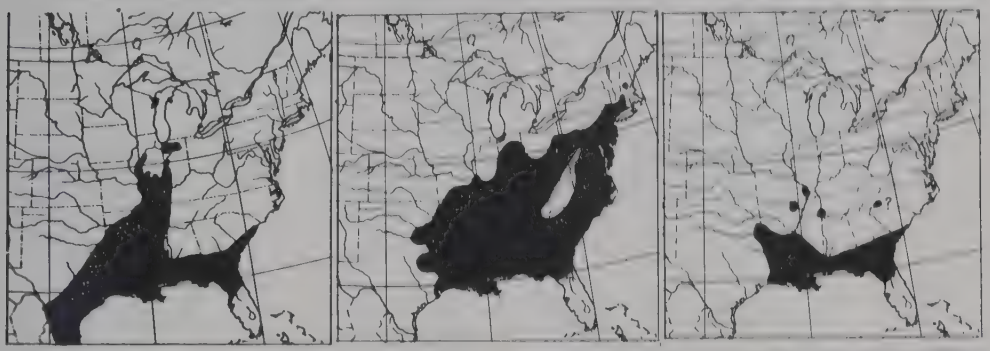

FIG. 13. RANGE OF SIREN INTERMEDIA. FIG. 14. RANGE OF AMBYSTOMA OPACUM. FIG. 15. RANGE OF AMBYSTOMA TALPOIDEUM.

FIG. 16. RANGE OF CEMOPHORA DOLIATA. FIG. 17. RANGE OF CROTALUS HORRIDUS. FIG. 18. RANGE OF CARPHOPHIS AMOENA.

well distributed in unglaciated areas, although many of them undoubtedly soon disappeared.

The Climatic Optimum (warm, moist period) and its effects

As the glaciers continued to retreat northward, as temperatures increased and growing seasons lengthened, a gradual northward advance of the flora and fauna can be envisioned. The major vegetational phases in eastern United States indicated by pollen profiles were pine followed by a more mesophytic association. Presumably the warming trend reached its height in the Climatic Optimum at which time there is reason to believe that the fauna of eastern United States was more southern in composition than at present. During this period northern or heat-intolerant species could be expected to have been eliminated unless they were able to move northward or find suitable habitat in local areas which provided some of the ecological characteristics of more northern areas. Certain boreal species did survive as remnants in local areas and are recorded by the relict colonies, Figures 2 to 8.

If during the Climatic Optimum southern animals were more widely distributed at northern lati

tudes than at present, we should expect evidence in the nature of relict populations well to the north of the main ranges of southern species, and this is the case.

The narrow-mouthed toad, *Microhyla carolinensis* (Fig. 10), is a striking example in the Mississippi Valley. Both the population in southeastern Iowa and in southwestern Illinois are almost certainly isolated from the main range of the species, and the colony in Illinois is so successful that specimens can be secured on almost every visit to the area. The cottonmouth, *Agkistrodon piscivorus* (Fig. 11), has a range indicating a more northern distribution in the past. The population at Chillicothe, Missouri, is well established, and a small colony in Illinois just south of St. Louis is apparently limited to an area not wider than two miles but appears to be holding its own.

A population of the eastern mud turtle, *Kinosternon subrubrum* (Fig. 12), and probably also that of a salamander, *Siren intermedia* (Fig. 13), appear to be Climatic Optimum relicts persisting in the sand areas of northwestern Indiana. The marbled salamander, *Ambystoma opacum* (Fig. 14), has a small but seemingly disjunct population in extreme northwestern Indiana and adjacent Michigan. The mole salamander, *Ambystoma talpoideum* (Fig. 15), and scarlet snake, *Cemophora doliata* (Fig. 16), if judged from the scanty distributional information available, each have three or more small relict populations well to the north of the main ranges of the species. Two other reptiles, the timber rattler, *Crotalus horridus* (Fig. 17), and eastern worm snake, *Carphophis amoena* (Fig. 18), deserve mention, but it is not certain that these apparent relicts reflect the Climatic Optimum. Both species have small colonies on the southern edge of Lake Erie, suggesting that their ranges once extended through Ohio to that latitude. There is however some possibility that the rattlesnake actually moved into northern Ohio via New York and southern Ontario rather than being left as a relict, and there is a possibility that the Erie County, Ohio, population of worm snakes is an accidental introduction by man.

Another type of evidence supporting the assumption that southern animals occurred farther north in the past than they do at present is provided by the discovery of remains of the rice rat, *Oryzomys palustris* (Fig. 19), in Indian Mounds near Peoria, Illinois, a locality approximately 200 miles north of the present range in the Mississippi Valley of this austroriparian species. Although this fossil evidence is perhaps open to question, the initial assumption that the rice rat occurred as far north as the Peoria area is now a distinct possibility.

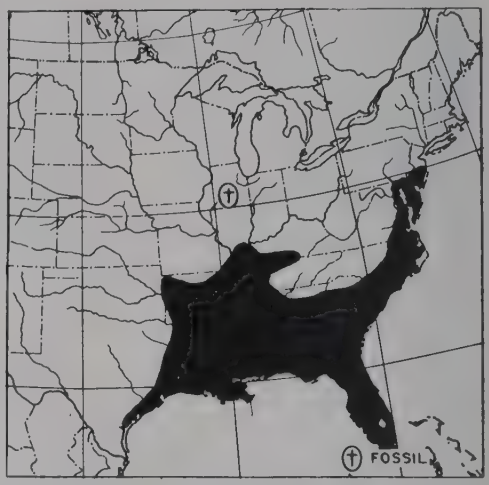

FIG. 19. Range of *Oryzomys palustris*.

Reviewing the illustrations presented thus far, it is difficult to account for the presence of ten species of animals so far removed from the main body of their ranges except by assuming a more northern distribution for each sometime in the past. All of the ten species are forest-inhabiting animals, and six of them are characteristic of swamp or floodplain forest habitats. This information permits the inference that during the Climatic Optimum not only were temperatures higher than at present but the climate may also have been warmer, and floodplain or at least mesic forest may have been more extensive and hence available for a northward dispersal by swamp-inhabiting animals. The relatively large number of pollen profiles for this period which show an abundance of elm, a stream-edge tree, the presence of beech in Iowa, and hemlock in areas where it no longer occurs, also suggests a wet climate.

Summarizing the reasoning thus far presented, we may conclude that the fauna of the Prairie Peninsula at the time of the Climatic Optimum was probably a more southern type than exists in the region today but that scattered boreal relicts were present in localized habitats, perhaps near bogs and cold streams. Probably the fauna was primarily a forest or forest-edge type, consisting of components which are now regarded as eastern and southern.

The Xerothermic period

With the approach of the equally warm but more arid Xerothermic period, the ranges of spe-

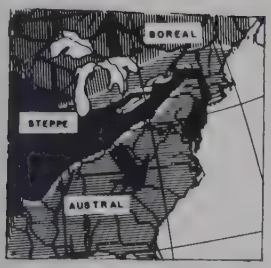

FIG. 20. XEROTHERMIC PERIOD.

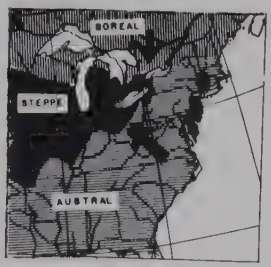

FIG. 21. WANE OF XEROTHERMIC PERIOD.

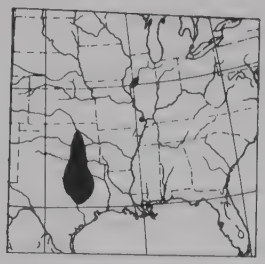

FIG. 22. RANGE OF PSEUDACRIS STREckERI.

FIG. 23. RANGE OF KINOSTERNON FLAVESCENS. FIG. 24. RANGE OF HETERODON NASICUS. FIG. 25. RANGE OF TERRAPENE ORNATA.

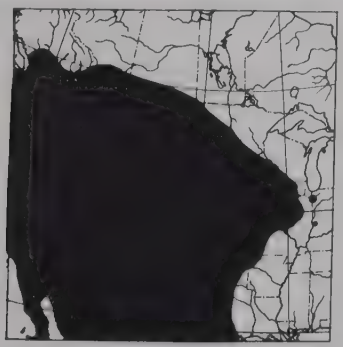

FIG. 26. RANGE OF PITUOPHIS CATENIFER.

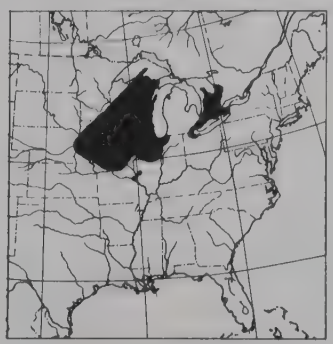

FIG. 27. RANGE OF ELAPHE VULPINA.

cies intolerant of aridity presumably shrank to the north and to the south of the gradually encroaching oak-hickory forest and the following grassland as they moved eastward within the Prairie Peninsula. The time of this arid phase has been inferred by stratigraphers as between 4,000 and 2,000 B.C. The recent radiocarbon dating of Zumberge and Potzger (1955) sets the maximum for the Xerothermic period as shortly after 4,000 years ago and is thus in remarkably close agreement with the estimated date. Whatever the duration of the arid period, it is believed that sufficient time elapsed for an eastward dispersal of plains plants and animals (Fig. 20). At the height of this dry phase, a few of the western components apparently reached as far east as the Atlantic Coast.

Evidence provided by relict populations

Although grassland and generally more arid conditions which prevailed during this phase must have resulted in some shrinking to the north and south of the ranges of mesic forest organisms, there is evidence that many refugia existed throughout the Xerothermic period. In these areas which may have been gallery forest or "islands" of forest within a predominantly grassland landscape, at least ten mesic-forest-inhabiting vertebrates (the Climatic Optimum relicts, Figs. 10 to 19) presumably persisted *in situ* inasmuch

as they are still present today. The small number of boreal relicts which exists at the present time also survived this most trying period in local refugia. Still other refugia were undoubtedly present, traces of which have since vanished, and it is reasonable to assume that the Great Lakes and major rivers may have afforded local conditions in which mesic forest animals could have survived the long period of drought. If the region near the confluence of the Ohio and Mississippi rivers were a refugium, the wealth of austroriparian animals in southern Illinois today is not surprising. Many species of southern animals extend northward along the eastern coastal plain and up the Mississippi Valley. On the east coast this is to be expected because a comparatively moderate climate also extends northward along the coastal plain, but in the colder Mississippi Valley it is difficult to account for the great number of distinctly southern species now present unless a refugium is postulated for the area. If the Climatic Optimum relict populations survived the Xerothermic period in the floodplain swamps of the Mississippi River, however, we need not make the rather unlikely assumption that these species re-ascended the Mississippi Valley within the past 3,000 years (the approximate length of time since the wane of the Xerothermic phase).

Returning to the grassland animals which we assume to be western immigrants that dispersed eastward during the arid phase, we should expect to find distributional evidence indicating a widespread western fauna within our limits during the Xerothermic. This evidence is abundant and extremely difficult to refute. As a cooler, moister climate returned to much of eastern North America, forest of a more mesic nature encroached onto the steppe, restoring habitats for animals characteristic of the eastern deciduous forest and eliminating habitat of grassland and oak-hickory forest (Fig. 21). Some of the grassland species probably disappeared from the area east of the Mississippi River. A few of the more ecologically tolerant animals were able to survive in the east only in the sand prairies where edaphic features approximated those of their original habitat.

The present ranges of Strecker's chorus frog, *Pseudacris streckeri* (Fig. 22), the yellow-necked mud turtle, *Kinosternon flavescens* (Fig. 23), and the western hognosed snake, *Heterodon nasicus* (Fig. 24), clearly illustrate animals which have been almost eliminated within the Prairie Peninsula since the wane of the Xerothermic period. The hiatus between the sand prairie populations and Great Plains populations in these three species varies from two to four hundred miles. Two other animals, the ornate box turtle,

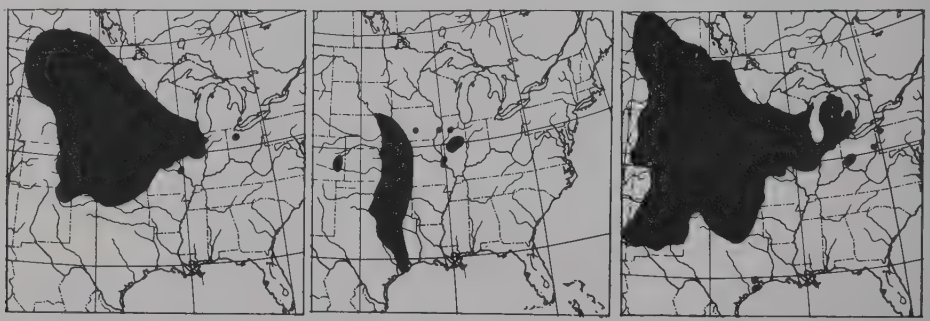

FIG. 28. RANGE OF THAMNOPHIS RADIX. FIG. 29. RANGE OF TROPIDOCLONION LINEATUM. FIG. 30. RANGE OF CITELLUS TRIDECEMLINEATUS.

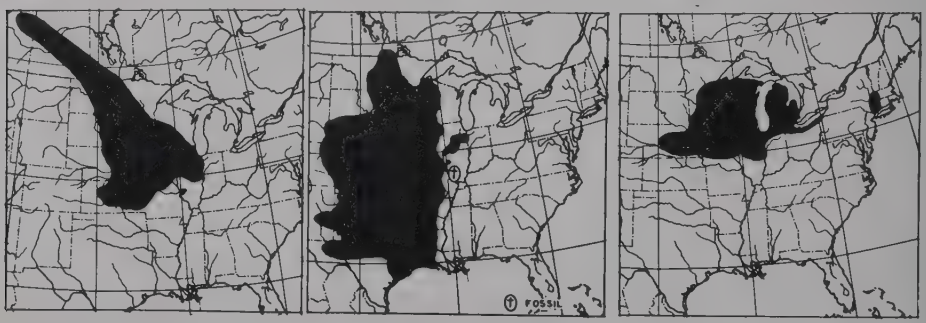

FIG. 31. RANGE OF CITELLUS FRANKLINI. FIG. 32. RANGE OF GEOMYS BURSARIUS. FIG. 33. RANGE OF EMYS BLANDINGI.

Terrapene ornata (Fig. 25), and the bullsnake, *Pituophis catenifer* (Fig. 26), also Xerothermic relicts, reach their easternmost limits of distribution in sand prairies, but they appear slightly more tolerant of humid prairie. Three species of prairie snakes are not restricted to sand but occur in grassland relicts well to the east of the main segments of their respective ranges. These are the fox snake, *Elaphe vulpina* (Fig. 27), the plains garter snake, *Thamnophis radix* (Fig. 28), and the lined snake, *Tropidoclonion lineatum* (Fig. 29). Three species of small mammals, the 13-lined ground squirrel, *Citellus tridecemlineatus* (Fig. 30), Franklin's ground squirrel, *Citellus franklini* (Fig. 31), and the pocket gopher, *Geomys bursarius* (Fig. 32), reflect a similar history. Blanding's turtle, *Emys blandingi* (Fig. 33), is possibly still another example, although the disjunct range of this reptile, like that of *Natrix kirtlandi* (Fig. 7), could be as readily interpreted as a boreal relict. In all likelihood there were additional Xerothermic relicts within the Prairie Peninsula, some of which persisted until as late as this century but were apparently erased by human activities. Civilization in all probability thus simply accelerated the eradication of populations probably doomed by climatic change.

Other evidence of the Xerothermic period

Turning to evidence other than that furnished by relict populations, the same general conclusions are suggested. The pocket gopher (Fig. 32) at the present time is restricted east of the Mississippi River to two rather small populations in Illinois and Indiana, but the recent discovery of abundant skeletal material of this species in Indian kitchen middens in Randolph County, Illinois, demonstrates that the gopher occurred commonly in this part of southern Illinois when the Indians buried the remains. Unfortunately, no date is as yet available for the archeological material.

Evidence of another sort is afforded by trends in geographic variation in several species of amphibians and reptiles. These variational anomalies, which are otherwise extremely confusing, can be readily explained on the basis of postglacial biogeography. Two snakes, the copperhead, *Agkistrodon contortrix* (Fig. 34), and the copperbellied water snake, *Natrix erythrogaster* (Fig. 35), each have an eastern and southern subspecies meeting and interbreeding in southern Illinois and parts of adjacent states. In both examples, however, small populations similar to the southern Gulf coastal race occur in the middle Mississippi and lower Illinois River valleys of Illinois, and these populations are geographically and genetically separated from the southern subspecies by an intergrade population (Figs. 34, 35). In the light of the faunal history suggested herein, we can envision the southern races extending up the Mississippi and Illinois River valleys to at least the northernmost localities for the species at the time of the Climatic Optimum. We can assume the snakes in central Illinois survived in a refugium while those in adjacent areas probably shrank to the south of the encroaching arid climate and grassland habitats. After the Xerothermic period when eastern animals of mesic forest again occupied much of their original ranges, secondary contact and intergradation between the eastern race and the relict populations in central Illinois was re-established. Since these two species are largely

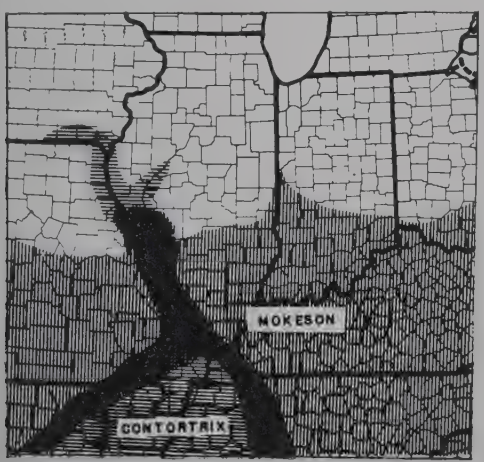

FIG. 34. DISTRIBUTION OF TWO SUBSPECIES OF AGKISTRODON CONTORTRIX.

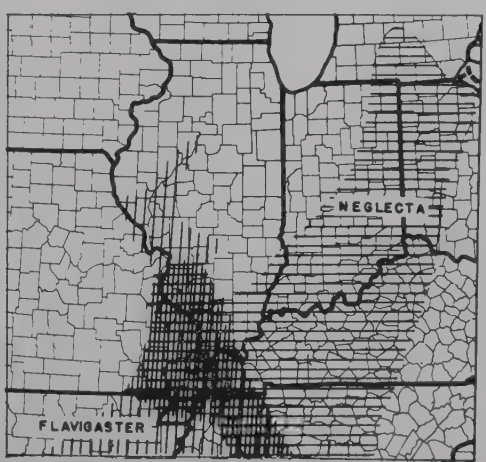

FIG. 35. DISTRIBUTION OF TWO SUBSPECIES OF NATRIX ERYTHROGASTER

restricted to river valleys and river bluffs in the predominantly prairie region of Illinois, a complete swamping out of the genes of the southern race in the relict populations has thus far been prevented by the relatively brief period of time the populations have been contiguous and by the narrowness of the corridor through which genes of the eastern race are able to infiltrate into the relict colonies.

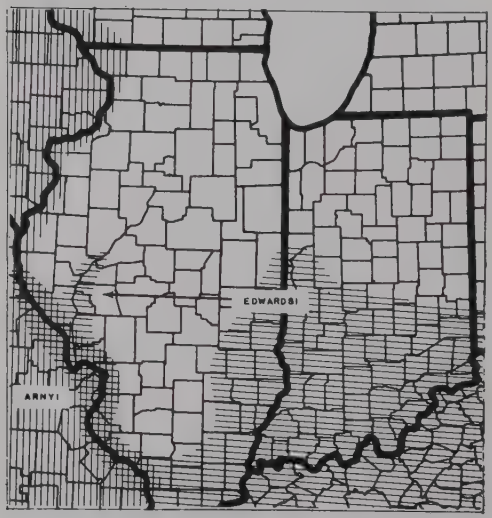

FIG. 36. Distribution of two subspecies of *Diadophis punctatus.*

A somewhat parallel situation can be seen in the ring-necked snakes, *Diadophis punctatus,* in Illinois. The variational peculiarity in this species is best seen by examining Figure 36. A widespread subspecies of the eastern deciduous forest (*D. p. edwardsi*) ranges to extreme eastern Illinois, traverses the southern tip of the state, and intergrades with a western subspecies (*D. p. arnyi*) in a narrow zone along the Mississippi River bluffs northward as far as Iowa, where genetically pure *arnyi* replaces the intergrade population. In the lower Illinois River bluffs, however, an apparently pure population of *edwardsi* occurs as a relict. It is separated from other *edwardsi* populations either by a large area of unsuitable habitat or by an intergrade population. The conclusion is inescapable, if we believe that the characters of *edwardsi* are genetic, that this eastern subspecies once extended as far west as the Illinois River but has since disappeared from the prairies of central Illinois. As in the two preceding examples, the preservation of the pure race in relict colonies is probably a function of time and the narrowness of the corridor through which foreign genic material can penetrate the relict population.

Another illustration which promises to be instructive is the range of the smooth green snake, *Opheodrys vernalis* (Fig. 37). This species consists of a western grassland race (*O. v. blanchardi*) and an eastern forest race (*O. v. vernalis*). The western *blanchardi* is widely distributed in the mountain meadows and tall grass prairies. An indication of how extensive its range may have been in former times is shown by the relict populations of this race in southwestern Ohio, southern Illinois, and in the Gulf coastal prairies of eastern Texas. Prior to the Xerothermic period the eastern forest race, *vernalis,* must have had a larger distribution inasmuch as a population in the forested Black Hills region of South Dakota is practically identical with eastern *vernalis,* even though it is essentially surrounded by *blanchardi.* Contact and interbreeding between the two races are known from Manitoba, Minnesota, Wisconsin, and Ohio at present. There are large areas within the Prairie Peninsula where apparently neither form occurs today.

Still another illustration from the field of geographic variation can be cited; like the preceding examples, this peculiarity apparently has only one satisfactory explanation. The chorus frog, *Pseudacris nigrita* (Fig. 38), includes two wide-ranging subspecies in eastern North America. A predominantly eastern, forest-inhabiting race, *P. n. feriarum,* extends from southern Pennsylvania down the Piedmont plateau and thence westward to eastern Texas. An essentially western, grassland race, *P. n. triseriata,* extends from extreme southern Ontario, westward through the Prairie Peninsula to central Kansas. The two subspecies meet and intergrade in a relatively broad belt from northeastern Texas to southern Indiana; elsewhere they are not in contact. At the northeastern extremity of the range of *feriarum,* a population occurs which is exceedingly close morphologically to *triseriata.* This small population, which inhabits the New Jersey and Del-Mar-Va peninsulae, was regarded as a peripherally varying infrasubspecies of *feriarum* by Smith and Smith (1952), but it has recently been split off and named *P. n. kalmi* by Harper (1955). At the northeastern edge of the range of *triseriata* in southern Ontario and the adjacent United States, a population occurs which is intermediate between *triseriata* and *feriarum.* Morphologically these intermediates suggest intergrades, but there is no geographically adjacent population of *feriarum* with which the frogs might interbreed to account for the suggested *feriarum* influence.

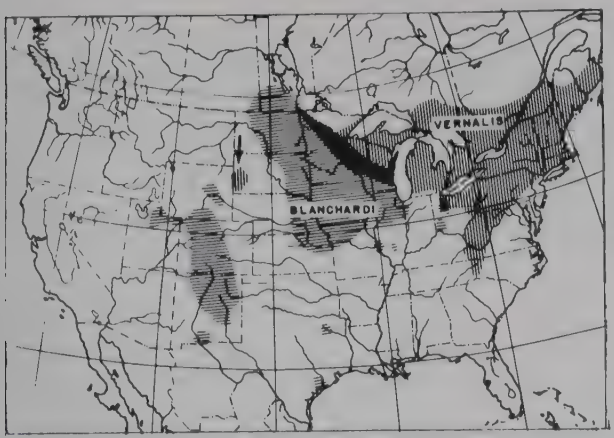

FIG. 37. DISTRIBUTION OF TWO SUBSPECIES OF OPHEODRYS VERNALIS.

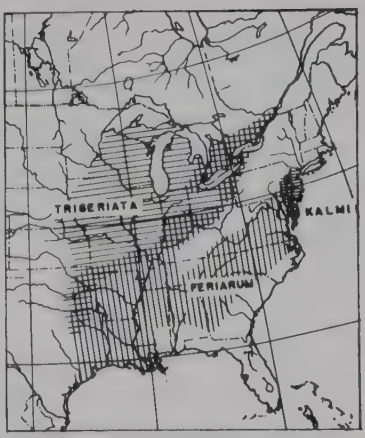

FIG. 38. DISTRIBUTION OF TWO SUBSPECIES OF PSEUDACRIS NIGRITA

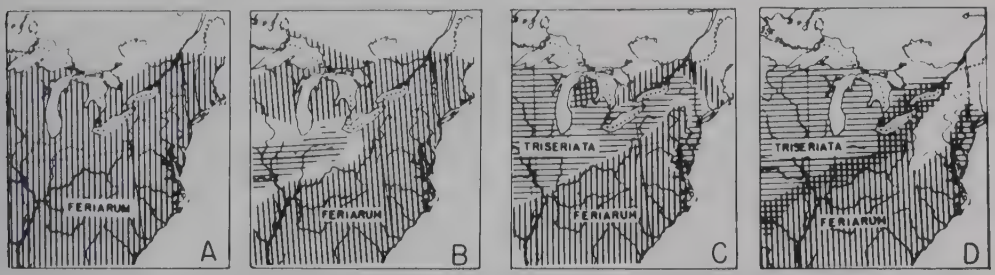

FIG. 39. POSTULATED DISTRIBUTIONAL RELATIONSHIPS OF PSEUDACRIS NIGRITA SUBSPECIES WITHIN PRAIRIE PENINSULA. A. CLIMATIC OPTIMUM, B. EARLY XEROTHERMIC, C. XEROTHERMIC MAXIMUM, D. POST-XEROTHERMIC.

A rather involved but plausible explanation for this situation is presented by the four diagrammatic maps (Fig. 39). During the Climatic Optimum the forest-inhabiting race, *feriarum*, was probably widespread in eastern United States. Its range was subsequently bisected by the eastward extension of grassland, which also enabled the prairie *triseriata* to reach New Jersey. During and following the Xerothermic period, the segment of *feriarum* range in southeastern Canada interbred with *triseriata*, and the *feriarum* characters in these populations have been almost swamped out by genes of *triseriata*. The populations in New Jersey and Del-Mar-Va (*P. n. kalmi*), which represent a derivative of Xerothermic *triseriata*, have not been as much affected by interbreeding with geographically adjacent *feriarum* because both are peninsular colonies, and the portals through which gene exchange might occur are quite narrow.

A situation involving three of the subspecies of the milk snake, *Lampropeltis triangulum* (Fig. 40), may parallel the geographic variation exhibited by *Pseudacris nigrita*. Roger Conant (pers. comm.) has called my attention to the very close similarity between the Del-Mar-Va race (*temporalis*) and a western race (*syspila*). The area between the ranges of these two subspecies is occupied by a third, and more distinctive, race (*triangulum*). If *temporalis* should prove to be a derivative of *syspila* that has been isolated only since the Xerothermic period, the steps outlined in the preceding paragraph could easily account for the great resemblance between the two widely separated populations.

As a review of the distributional evidence indicating a rather recent withdrawal to the west of a large grassland fauna in the Prairie Peninsula, a composite map (Fig. 41), which shows all of the known Xerothermic relicts, is presented. It is readily seen that a few forms penetrated to the east coast. In the case of *P. n. kalmi* (Fig. 38), a complete swamping out of the characters of the Xerothermic immigrant has been postponed by the occurrence of these populations on peninsulae. Toward the west the number of Xerothermic relicts increases, suggesting that some western components were able to extend farther east in the

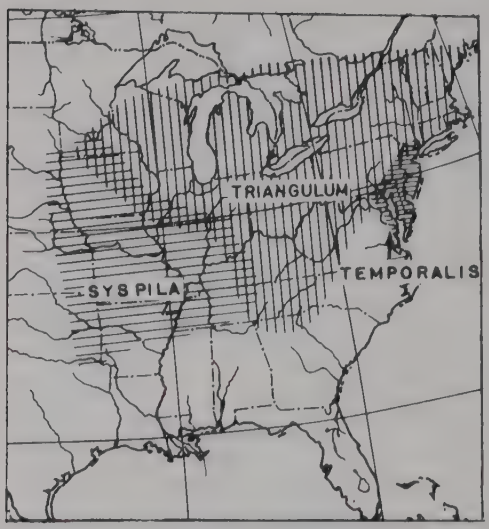

FIG. 40. Distribution of three subspecies of *Lampropeltis triangulum*.

Prairie Peninsula than others and that the subsequent reduction of grassland habitat has been less pronounced toward the west. It is noteworthy that the boundaries of these relict colonies often coincide in Indiana and Illinois where the prairie habitats begin to resemble those of our more western grasslands and presumably are similar to those habitats which were more widespread in the Prairie Peninsula during the Xerothermic period.

The post-Xerothermic or recent period

It is now necessary to re-examine all distributional patterns of animals, whether or not they include relicts, in light of the postulated post-Wisconsin chronology. The pollen profiles show that either deciduous forest trees, conifers, or both have recently invaded the eastern and northern portions of the Prairie Peninsula, entirely covering the pollen deposits of the arid and warmth-loving oak-hickory forests. Although pollen data for Indiana and Illinois come primarily from bogs that are truncated at the top and thus cannot show a similar forest replacement, it is only necessary to drive through these two states to see that forest trees of a more mesic nature are well established in much of Indiana as well as in eastern Illinois and to note that Illinois is, or was before intensive cultivation, primarily grassland. Accordingly, it should be possible to visualize the faunistic events occurring today, and in this connection a number of distributional patterns are instructive.

Several predominantly northern animals have ranges that can be interpreted as having extended varying distances southward into the forested parts of the Prairie Peninsula since the appearance of the present cooler, more humid climate. The main segments of the ranges of those species with boreal relicts (Figs. 2 to 8), have in all likelihood re-occupied parts of the Prairie Peninsula which were chiefly grassland during the Xerothermic period. Many other species could be mentioned which belong in the same category.

An imposing list of eastern forest animals can be envisioned as having been derived from the east and southeast. Those vagile species with wide temperature tolerances appear to have re-entered the forested parts of Indiana and Illinois from both a northeasterly and southeasterly direction, circumventing the central prairie regions. In a few cases, dispersals both up and down the now forested valleys and bluffs of the Mississippi River approach each other (*vide* the spotted salamander, *Ambystoma maculatum*, Fig. 42, and the wood frog, *Rana sylvatica*, Fig. 3.) In other cases, the populations ascending and descending the forested valleys and bluffs of the Mississippi have met so that interbreeding populations encircle rather large areas that are uninhabited by these animals (*vide* the pickerel frog, *Rana palustris*, Fig. 43, and the green frog, *Rana clamitans*, Fig. 44). Species with a somewhat greater ecological tolerance have apparently successfully repopulated a large portion of the forest habitats (*vide* the newt *Diemictylus viridescens*, Fig. 45, and the lesser five-lined skink, *Eumeces fasciatus*, Fig. 46).

It would seem that the strictly southern species (the austroriparian components) are not greatly affected by the present climatic phase. Although they probably enjoy the advantage of newly available forest habitat in which they might expand, they are limited somewhat by temperatures which are lower than those existing during the Climatic Optimum.

It is extremely difficult to ascertain the effect of the present climate on a great many of our animal populations inasmuch as habitats within the Prairie Peninsula region have been so greatly altered by human activity. Continuous land cultivation, destruction of forest, drainage of bogs and marshes, and general lowering of the water table have obviously had a major effect upon animal distribution. These changes, although minor from a temporal viewpoint, have undoubtedly obscured many of the trends which we might otherwise expect to see illustrated by distributional patterns.

The foregoing synthesis has been concerned wholly with post-Wisconsin distributional con-

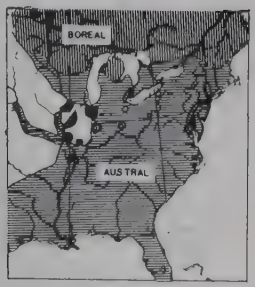

FIG. 41. COMPOSITE OF XEROTHERMIC RELICTS.

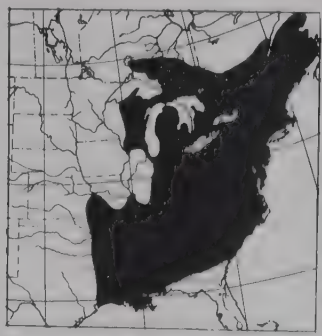

FIG. 42. RANGE OF AMBYSTOMA MACULATUM.

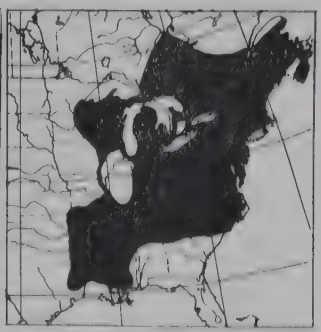

FIG. 43. RANGE OF RANA PALUSTRIS.

FIG. 44. RANGE OF RANA CLAMITANS.

FIG. 45. RANGE OF DIEMICTYLUS VIRIDESCENS.

FIG. 46. RANGE OF EUMECES FASCIATUS.

siderations. Several bits of evidence that may contribute significantly to our knowledge of speciation and subspeciation are immediately apparent, and speculation upon the origin of the taxa, their sites of differentiation, and their comparative evolutionary rates becomes extremely tempting. The events which led to the development of species and races can be postulated in greater detail and with more certainty, however, when our understanding of the post-Wisconsin biogeography is more refined. It is hoped that this essay will stimulate others to test the hypothesis presented herein by an analysis of distributional phenomena that I have overlooked or that I have omitted because of my inability to interpret them properly.

Summary

During the Wisconsin glacial maximum the pre-existing biota of northeastern North America was displaced to the south. Following the retreat of the ice front the glaciated region was re-occupied by a northward-dispersing flora and fauna. The present vertebrate fauna of the Prairie Peninsula suggests, however, that rather profound climatic changes have occurred since deglaciation to produce the faunal complexity of the eastern United States. The distributional evidence provided by the terrestrial vertebrates permits generalizations remarkably parallel to inferences drawn from other biogeographic data, and the phenomena displayed by the vertebrates are readily explained by the post-Wisconsin chronology which is based largely on pollen data.

Evidence to support the presumed southward displacement of boreal components during the glacial maximum is afforded by the present disjunct ranges of three species of amphibians and four reptiles. The species have ranges partially or wholly within glaciated North America and have conspicuous relict populations well to the south of the main segments of their ranges.

According to the accepted chronology the climate moderated after deglaciation, culminating in the so-called Climatic Optimum. The pollen profiles and other fossil evidence indicate a vegetational succession of tundra, spruce-fir, pine, and mesophytic forest. A more humid, as well as warmer, phase is indicated by the replacement of pine by such mesophytes as elm, beech, hemlock, and oak. At the height of the Climatic Optimum several southern components are believed to have dispersed northward well beyond the present northern limits of their continuous ranges. Evidence to support this assumption is provided by the present disjunct ranges of four species of amphibians and five reptiles, all of which have relict

populations well to the north of the main segments of their ranges. Additional evidence that southern elements once occurred farther north than at present is found in the presence of undated remains of rice rats in Indian mounds near Peoria, Illinois.

The Climatic Optimum, which herein is restricted to the warm, humid phase during which mesophytes predominate in the pollen profiles, was followed by the Xerothermic interval, during which time mesic forest habitats shrank to the east, north, and south of encroaching oak-hickory forest and expanding grassland habitats. Local refugia probably existed throughout the Xerothermic phase along the major rivers and Great Lakes as the Climatic Optimum relicts as well as the boreal relicts have survived *in situ* until today. The increasing aridity and replacement of mesic habitats by arid forest and grassland presumably permitted an eastern immigration by numerous western components. At the close of the Xerothermic period, the climate became cooler and more humid as it is today. The western components were either eliminated or reduced to small relict populations as their habitat retreated westward from encroaching mesic forest habitats. Evidence of formerly more widespread occurrence of western elements in the east is provided by relict populations of one species of amphibian, eight reptiles, and three small mammals. Additional evidence is afforded by the abundance of pocket gopher remains in Indian mounds in Randolph County, Illinois, where the species was apparently once common but has since disappeared.

Evidence of still another sort to support the postulated climatic shifts is illustrated by trends in geographic variation. Climatic Optimum relicts of four different species of snakes that have not had sufficient time to be swamped out completely through interbreeding with adjacent members of post-Climatic-Optimum populations are discernible through studies of geographic variation. In another species of snake and in a frog, variation trends strongly suggest the presence of Xerothermic relicts in the Del-Mar-Va Peninsula. Both small populations are recognizably distinct but probably are recent derivatives of western immigrants that dispersed eastward during the Xerothermic phase.

The present distributional patterns of many eastern forest animals suggest that this fauna is re-occupying the Prairie Peninsula wherever suitable habitat has reappeared. The dynamic dispersal of eastern species is particularly well shown by the various stages in the re-occupation of the forested Mississippi River valley and associated bluffs.

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A METHOD OF SAMPLING THE LITTORAL MACROFAUNA AND ITS APPLICATION[1]

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INTRODUCTION

The purpose of this work is to describe and test a method of separating the benthic macrofauna from the phytomacrofauna in the littoral zone of a lake. These two groups of animals can be distinguished quantitatively by removing the plants from a square frame about 90 cm high and sampling the benthos in the same area with an Ekman dredge. A more complete sample of the littoral fauna can be obtained in this way. Also, it is possible to study the relative contribution of the plants and the bottom to the total fauna and the factors affecting the quantity and distribution of various organisms. An illustration of the use of the sampler for these purposes is presented.

Benthos refers to the animals which live on the bottom. Phytomacrofauna defines the animals which live in association with the plants. It is necessary to make this distinction because the term benthos has been used rather loosely in reference to the littoral zone. All of the animals which are collected by a dredge have usually been referred to as benthos even though the plants and the mud are obviously different habitats. Phytomacrofauna is composed of the animals which cling to the stems and leaves, the forms which swim among the plants like the Hydracarina and Amphipoda, and the species which mine the various parts of the plants. The latter group have not been considered here because special sampling and handling techniques are required in order to study them. Fishes have been ruled out arbitrarily.

The requirements for taking separate samples of the benthos and phytomacrofauna at the same time and place are: (1) the plants must be removed first, and (2) the bottom should be undisturbed. Three methods have been described for the collection of plants. Ball (1948) used a "plant hook" which grabbed plants as it was drawn through the water, and McGaha (1952) mentions a similar method. Rosine (1951) waded among submerged plants, broke the stems by hand, and gently eased them into a fine-meshed dipnet. Andrews and Hasler (1943) designed a canvas bag which could be lowered over the plants. A zippered side enabled the operator to reach in and detach the plants from the bottom. The bag was closed and lifted from the water with the plants inside. The plants are torn out by the roots during the operation of the plant hook and the canvas bag, and neither method would provide an undisturbed sample of the bottom. The dipnet method of Rosine is not adapated for quantitative collection in a circumscribed area and probably does not sample the animals swimming among the plants completely.

Several types of dredges have been used to sample the littoral fauna. A hoe dredge was designed by Scott, Hile, and Spieth (1928, 1938) for their work in Wawasee and Tippecanoe lakes, Indiana, and a somewhat similar apparatus was used by Rawson (1930) in Lake Simcoe, Ontario. A dredge of the Ekman or Petersen design has been used extensively in recent years. Ball (1948, 1949) and Eggleton (1952) employed both types in their work on Michigan lakes. Wohlschlag (1950) and Deevey (1941) mounted an Ekman dredge on a pole or rod. None of the dredges separates the benthos and phytomacrofauna. In addition, the roots of plants may prevent the dredge from penetrating far into the mud. The pole-mounted Ekman and the Petersen dredge overcome this difficulty. However, the plants dangle from the jaws when either type of dredge is used, and the animals which cling to the plants are partially lost as the dredge is hauled to the surface. Also, the plants usually prevent a tight closure of the jaws as Rawson (1930) mentioned.

THE SAMPLING METHOD

Description of the sampler. Two models of the sampler have been built. Each one is described since both models were used in the experiments which follow. Model A is a 44.5-cm (inside dimension) square frame which extends 70.5 cm above a metal base (Fig. 1). The frame is constructed with ¾ inch wood supports and lined with copper screening. The metal base has a 10-cm flange and a slot into which fits a screen-covered "sliding door."

Model B is made entirely of galvanized sheet metal. It is similar to Model A in its general design, but consists of two square shells, one fitting inside the other (Fig. 2). The inner shell is 27.5 cm square and 77.0 cm high. It has a slot at the base. The outer shell is 32.5 cm square

[1] Contribution No. 603 from the Department of Zoology of Indiana University. The Research Committee of the University, The Graduate School and the National Science Foundation all provided grants which contributed to the work. Their cooperation is greatly appreciated.

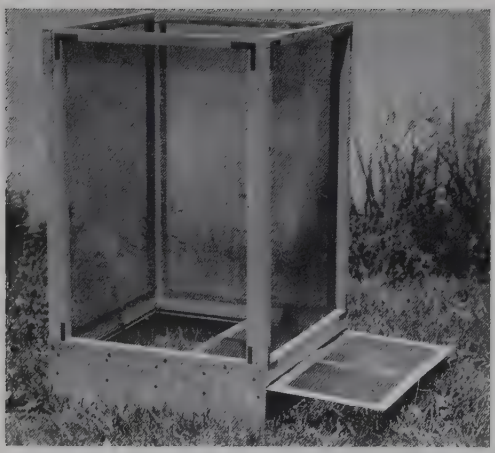

FIG. 1. Model A sampler constructed in 1953 for the study of the littoral macrofauna.

and 77.0 cm high above a metal stop. An 11.5-cm flange extends below the stop. When the inner shell rests on the stop, a sliding door can be fitted into the slot. A 14-mesh bronze screen is soldered to the four sides of inner shell and the sliding door.

Operation of the sampler. The sampler is placed over a stand of vegetation and secured to the bottom by pressing the flange into the mud. The plants are cut with a pair of grass clippers as close to the mud surface as possible. The plants are handled carefully so that the organisms clinging to them will be disturbed as little as possible. Following the clipping operation, the sliding door is pushed securely into the slot, thereby separating the phytomacrofauna from the benthos.

The operation of the two models is the same up to this point. After the sliding door is in position, Model A is lifted from the water. The plants are removed and placed in a bucket partially filled with water. Rinsings are poured into the same container. The bottom was disturbed somewhat by raising the sampler, and Model B was designed to overcome this difficulty. The inner shell, containing the plants, is raised, and the outer shell remains in place.

The benthos is sampled with a 15-cm-square Ekman dredge which is placed in the area from which the plants have been removed. When using the Model B sampler, the dredge is lowered inside the outer shell. The dredge is seated firmly into the mud by hand in order to prevent roots from interfering with the jaw closure. The closure is checked by hand before removing the

FIG. 2. Model B sampler constructed in 1955 for the study of the littoral macrofauna.

sample. The mud and rinsings from the dredge are placed in a separate container.

If the sampling operation is performed carefully, the phytomacrofauna and the benthos are separated cleanly. The chief disadvantage of the sampler is that it cannot be used in water deeper than about 1 meter, although plants frequently grow at greater depths. Plants with erect stems are very easy to sample. Prostrate plants offer little difficulty as the sharp flange at the base of the sampler cuts through the stems easily.

Handling the samples in the laboratory. A few preliminary samples were taken to experiment with methods of washing the animals off the plant. A forcible spray of water did not remove some of the clinging organisms like leeches. When formaldehyde was added to the water a few hours before washing, these organisms were found. This practice also reduced predation.

After formaldehyde treatment, the plants were washed individually with a spray of water into a series of graded sieves. U. S. Standard Sieves were used; no. 6 with a mesh opening of 3360 microns, no. 16 with 1160-micron meshes, and no. 35 with 500-micron meshes. The larger organisms

remained in the no. 6 sieve, but most of the animals were concentrated in the other two sieves. The material from the no. 16 sieve was inspected by eye in a white enamel pan. The washings on the no. 35 sieve were examined under a binocular microscope.

The plants were air-dried after washing and weighed on a triple-beam balance sensitive to 0.1 g in order to relate the macrofauna to the quantity of plants.

The bottom samples were handled with the organisms alive. These samples were sorted by eye, checking occasionally with the binocular microscope to be sure that no significant oversight was being made.

The organisms were counted, sorted, and stored in 70 per cent alcohol. Identification to genus was made in most cases and the species was determined for some organisms (see Appendix).

Comparison of Sampling Methods

Soon after the Model B sampler was built in 1955, two experiments were done to compare it with other methods which have been used in the littoral zone. These experiments were not intended to be exhaustive, but they are instructive as a preliminary test of the sampler. The collections were made on July 9, 1955, in the bay opposite the Indiana University Biological Station at Winona Lake, Indiana. A dense stand of *Ceratophyllum demersum* was sampled in 70 cm of water on a soft mud bottom.

Phytomacrofauna collected with the plant hook and with the Model B sampler. The plant hook was a 20-cm piece of one-half-inch pipe with four 40-cm pieces of heavy gauge wire thrust through it and bent backward. The hook was thrown about 20 feet from a boat, and the plants were grabbed as the hook was hauled through the water. A screened-bottom pan was held beneath the plants as they were lifted into the boat. Duplicate samples were taken with both the hook and the Model B sampler. The phytomacrofauna was counted and comparisons were made between the two methods on the basis of the number of organisms per gram of air-dried plant.

The Model B sampler collected 114 organisms per gram of *Ceratophyllum*, and 70 were taken by the hook (Table I). Of 12 types of invertebrates, 10 were more numerous in collections made by the sampler than in those made by the hook. These include the active swimmers as well as the clinging organisms.

Fauna collected by the Ekman dredge alone and with the Model B sampling method. Duplicate samples were taken with the Ekman dredge alone and with the Model B sampler. The number of animals per 1000 sq. cm. of bottom was used as a basis of comparison.

Table I. Comparison of the littoral fauna collected by three sampling methods. The samples were taken in a bed of *Ceratophyllum demersum* in Winona Lake, Indiana. Values are averages of duplicate samples

Organism	Plant hook	Model B Sampler			Ekman dredge Combined faunas
		Phytomacrofauna		Benthos	
	No./g plant	No./g plant	No./1000 sq. cm	No./1000 sq. cm	No./1000 sq. cm
Turbellaria	1.2	1.8	27	45	11
Oligochaeta	1.4	3.8	49	43	22
Hirudinea	0.0	0.1	1	0	0
Cladocera and Copepoda	0.3	0.4	5	2	0
Amphipoda	32.7	37.7	533	88	164
Hydracarina	0.1	0.4	6	0	0
Ephemeroptera	4.7	2.7	39	105	17
Odonata	0.1	0.1	1	0	2
Trichoptera	0.3	0.7	10	4	0
Coleoptera	0.0	0.0	0	2	2
Tendipedidae	30.0	66.8	946	230	382
Total	70.7	114.4	1617	579	600

The Model B sampler took the same number of benthic organisms as the combined samples of benthos and phytomacrofauna collected by the dredge alone (579 and 600 organisms per 1000 sq. cm, respectively). The presence of plants in the dredge hauls accounts for some of the differences between the two series of samples (Table I). The dredge alone took 92 more tendipedid larva and 76 more amphipods per 1000 sq. cm. than did the Model B sampler. Both of these organisms are more abundant on plants than in the mud. Oligochaetes were more abundant in the dredge hauls from the Model B sampler because the jaws were free to penetrate the mud. The difference in Ephemeroptera between the sampling methods was due to large variation among the samples.

The combined phytomacrofauna and benthos collected by the Model B samples was 2196 animals per 1000 sq. cm, as opposed to 600 taken by the Ekman dredge. This difference amply illustrates the inadequacy of this type of dredge for sampling the littoral macrofauna.

The Use of the Sampler

Description of the experiment. The experiment was performed in 1953 with the Model A sampler. Three species of submerged aquatic plants which differed in the size and shape of the leaves and in the extent of the root system were selected for sampling. *Anacharis canadensis* has oval-shaped leaves borne in whorls on an erect, slender, branched stem. It has a poorly developed,

adventitious root system. The slender stems of *Najas flexilis* have thin, filamentous leaves. The roots are delicate fibers. The ribbon-like leaves of *Vallisneria americana* rise in clusters from a creeping rootstock, and the relatively large roots anchor the plant firmly in the mud. The plants grew in Bryant's Creek Lake in the Morgan-Monroe County State Forest, 15 miles north of Bloomington, Indiana. The three species were located in a narrow band along 200 feet of shoreline. The depth of water varied from ½ to 1 meter.

Duplicate samples were taken in each species of vegetation. The collections were made twice during the summer, making a total of 12 plant and 12 mud samples. The *Anacharis* collections were made on June 25 and July 28; *Najas* on July 9 and August 6; and *Vallisneria* on July 20 and August 12.

The results are reported as dry weight of macrofauna. Individuals of each taxonomic category were counted into porcelain crucibles and dried to constant weight in a drying oven at 70° C. The crucibles were cooled and weighed to 0.1 mg on an analytical balance. There were too few specimens to determine dry weight in some cases, and weights of organisms of similar size were substituted.

Trichoptera were removed from their case before the dry weight was measured. The shells of molluscs, which were living at the time of collection, were dissolved with 10 percent hydrochloric acid as Holme (1953) did in his studies of the English Channel bottom fauna. An average weight loss of 90 percent accompanied the acid treatment. The body of the mollusc and the periostracum were dried and weighed as described above.

Qualitative comparison of the benthos and phytomacrofauna. The variety of organisms associated with the plants is much greater than the benthic fauna (Appendix). The benthos beneath *Najas* on July 9 contained several organisms which were rarely seen in the dredge samples. Some of the phytomacrofauna had obviously fallen to the bottom in one of the samples. With this exception, amphipods, water mites, mayflies, Odonata, true bugs, caddis flies, and beetles are almost completely lacking on the bottom, while all of these animals are well represented on the plants. The plants apparently offer a greater variety of habitat than the mud.

The organisms which are common to both the plants and bottom are found in quite different proportions in the two environments. Tendipedid larvae compose 58 percent of the plant fauna and only 8 percent of the benthos. The other Diptera occurred in greater proportion in the mud than on the plants. Oligochaetes averaged 5 percent of the phytomacrofauna and 60 percent of the benthos. Molluscs followed the pattern of the tendipedids.

TABLE II. The relation between the quantity of plants and the quantity of phytomacrofauna

	Dry weight of plants, g	Dry weight of organisms g x 10^{-5}
Anacharis	38.5	3422
	41.7	4949
	46.3	5267
	56.7	9664
Najas	26.3	4116
	29.6	4812
	34.1	5935
	42.5	10233
Vallisneria	26.6	4031
	27.9	4674
	28.4	4593
	28.6	4924

Quantitative analysis of the benthos and phytomacrofauna. The quantity of phytomacrofauna on each species of plant increases as the quantity of plants increases (Table II). Therefore, the dry weight of organisms per gram of air-dried plant was used to analyze for possible differences among the plants. Seasonal changes in the fauna could also be detected in the same computation by using the analysis of variance.

The quantity of phytomacrofauna was associated with the species of plant (Table III). The difference between the means of *Anacharis* and *Vallisneria* (14.5 x 10^{-5} g) was not statistically significant, but the *Najas* fauna (188.3 x 10^{-5} g) was significantly greater than that on the former plants (av. = 141.3 x 10^{-5} g).

The greater invertebrate fauna on *Najas* can be attributed to an excess of all of its components with the exception of the midge larvae. The dry weight of molluscs, Odonata, water mites, and amphipods was significantly greater on *Najas*, and the caddis-fly larvae and mayfly larvae showed the same preference. About one-third fewer midge larvae lived on *Najas* than on *Anacharis* and *Vallisneria*.

There was a significant seasonal increase of 34.2 x 10^{-5} g in the plant fauna. This was caused by a large increment in the dry weight of Mollusca and Odonata from the first to the

TABLE III. Summary of the analysis of the total quantity of the phytomacrofauna and of several of its components. Approximately one month elapsed between the first and second collections. Values are expressed as dry weight in grams x 10^{-5} per gram of plant

Source of variation	Total fauna	Tendipedidae	Mollusca	Odonata	Hydracarina	Trichoptera	Amphipoda	Ephemeroptera
Plant								
Av. *Anacharis*	134.0	91.3	8.5	8.7	3.1	1.7	0.7	0.8
Av. *Najas*	188.3	61.8	44.9	27.6	8.7	7.3	11.5	5.2
Av. *Vallisneria*	148.5	106.5	4.2	17.0	3.2	3.4	2.5	2.8
Mean square	6311.3**	2037.5*	2002.5**	356.9**	41.6**	32.2	133.5*	19.2
Season								
Av. 1st collection	139.8	81.7	12.1	14.7	5.7	3.7	2.5	1.4
Av. 2nd collection	174.0	91.3	26.2	20.8	4.3	4.5	7.2	4.5
Mean square	3502.2*	301.1	592.0**	112.2*	5.5	1.8	67.7	29.1
Mean square within plant samples	488.6	378.1	29.8	19.7	11.9	10.7	19.1	5.9

*Above 5 per cent level of significance.
**Above 1 per cent level of significance.

TABLE IV. Summary of analysis of the total quantity of the benthos and of several of its components. Approximately one month elapsed between the first and second collections. Values are expressed as dry weight in grams x 10^{-4} per 1000 square centimeters

Source of variation	Total benthos	Oligochaeta	Tendipedidae	Other Diptera	Mollusca
Plant					
Av. *Anacharis*	159.8	62.4	14.0	75.8	5.6
Av. *Najas*	495.0	180.6	46.9	130.0	48.2
Av. *Vallisneria*	1,150.0	982.5	35.9	93.9	24.3
Mean square	1,014,675.1*	1,008,360.6**	1,125.7**	3,051.0	1,787.6**
Season					
Av. 1st collection	637.7	422.6	46.9	118.0	35.1
Av. 2nd collection	565.5	394.5	19.6	81.4	17.0
Mean square	15,624.1	2,363.1	1,915.2**	3,927.7	930.7*
Mean square within samples	25,275.1	32,479.2	66.0	2,144.3	114.2

*Above 5 per cent level of significance.
**Above 1 per cent level of significance.

second collection, and the tendency of the Tendipedidae, Trichoptera, Amphipoda, and Ephemeroptera to increase to a slight extent. Hydracarina decreased a small amount.

The benthos was also influenced greatly by the plants (Table IV). The *Vallisneria* benthos (1150.0 x 10^{-4} g per 1000 sq. cm) was more than seven times greater than the *Anacharis* benthos (159.8 x 10^{-4} g per 1000 sq. cm), and more than twice as great as that found beneath *Najas* (495.0 x 10^{-4} g per 1000 sq. cm).

Oligochaetes were the most abundant benthic organisms. The variation among the plants was due principally to this group. There were 16 times more oligochaetes associated with *Vallisneria* than with *Anacharis* and five times more than with *Najas*. Statistically significant variations were also found in the tendipedids and molluscs, but these organisms were more abundant beneath *Najas*. The "other Diptera" showed the same tendency.

The seasonal decrease of the benthos (72.2 x 10^{-4} g per 1000 sq. cm) was not statistically significant because sampling variation was large. Midge larvae and molluscs decreased a significant amount in this respect, and the other components reflected a similar trend.

DISCUSSION

The Bryant's Creek Lake work has demonstrated that the new method of sampling can separate successfully the fauna of the plants and of the bottom in the shallow littoral zone. In addition to illustrating the effectiveness of the sampler, the results contribute modestly to two aspects of littoral productivity. The relative contribution of the bottom and plants to the total fauna was assessed by separate quantitative samples of the two habitats. Also, the types and abundance of animals were influenced by the characteristics of the roots and erect portions of the plants.

The benthos is correlated with the development

of the roots. *Vallisneria* has a more extensive root system and a greater quantity of benthos than the other two genera. *Najas* is intermediate in both respects followed by *Anacharis*. Plants stabilize the bottom (McGaha 1952), and stability is related to the degree of root development. Our results suggest strongly that the quantity of benthos is associated with the stability of the bottom.

Muttkowski (1918), Andrews and Hasler (1943), Entz (1947), Berg (1949), Krecker (1939), Rosine (1955), and Edmondson (1944) have all contributed to the study of the phytomacrofauna. The general conclusions of these studies have been as follows: (1) the phytomacrofauna is composed of a large number of species, (2) the abundance of certain organisms changes with the season, (3) the animals are generally more abundant near the surface than near the bottom, (4) plants with the more dissected leaves harbor a greater quantity of invertebrates, and (5) some animals are more numerous on certain species of plants than on others. These observations have been well documented and our findings supply only added confirmation. For example, *Najas* has a greater leaf surface than *Anacharis* or *Vallisneria,* and it has a greater fauna. Midge larvae provide an example of the preference of some animals for certain species of plants. They were three times more abundant on the latter two genera than on the former one.

The phytomacrofauna can be compared directly with the benthos by computing the quantity of animals on a standard weight of plants above a unit area of bottom. An average of 18.0 g dry dry weight of plants per 1000 sq. cm was collected, and this will be considered a standard unit for a dense stand of vegetation. The quantities of phytomacrofauna computed on this basis are: 2412, 3390, and 2675 x 10^{-5} g per 1000 sq. cm for *Anacharis, Najas,* and *Vallisneria,* respectively. The average quantities of benthos are: 1603, 4950, and 11500 x 10^{-5} g per 1000 sq. cm in the same order. The plant fauna composes 59 percent of the total quantity of invertebrates associated with *Anacharis,* 41 percent with *Najas,* and 23 percent with *Vallisneria.*

Pearcy (1953) found no difference in the numbers or volume of the invertebrate fauna between vegetated and barren, shallow water regions of Clear Lake, Iowa. This finding contrasts with the work of Wohlschlag (1950), Rawson (1934), and Edmondson (1944) who concluded that the fauna of vegetated areas was greater than that of barren areas. The results with the new sampling method support the latter conclusion, although a direct comparison was not made. Our experience implies that an area with a mixture of submerged aquatic plants would have about twice as many organisms as a non-vegetated zone.

Acknowledgments

Edward Mockford and Russell Noyes, Jr. helped with the original development of the sampler in 1950. When the work was taken up again in 1953, Roderick Turner and Jean Rogers Lowry did the sampling and sorting. Richard Mountjoy compared the sampling methods in 1955, and he very kindly consented to include his data in the paper. To all these persons, the author owes a debt of gratitude for their painstaking work.

Summary

A new method of sampling the littoral zone of lakes is presented as a renewed attempt to estimate the quantity of macrofauna in this complex part of the aquatic environment. The method differentiates the bottom dwelling animals, or benthos, from the organisms living in association with the plants, or phytomacrofauna.

The submerged aquatic plants are removed from a square frame which is about 90 cm high and open at both ends. The plants are clipped as close to the mud surface as possible and a sliding door at the base of the sampler is closed, separating the phytomacrofauna from the benthos without disturbing the mud. After the plants are removed, the benthos in the same region is sampled with an Ekman dredge.

The new system was superior to the Ekman dredge for estimates of the total fauna, and it was more efficient than a grappling hook for the collection of phytomacrofauna.

Samples were taken in *Anacharis canadensis, Najas flexilis,* and *Vallisneria americana.* Amphipods, water mites, mayflies, Odonata, true bugs, caddisflies, and beetles were almost wholly lacking in the benthos but were found commonly in association with the plants. Those organisms which are common to both the plants and the mud occurred in quite different proportions in the two habitats.

Najas had a greater fauna than the other two species. This was attributed to its large leaf surface. There was evidence of seasonal variation in abundance. Preference of some organisms for certain species of plants was demonstrated. Tendipedids were about one-third less abundant on *Najas* than on *Vallisneria* or *Anacharis.*

The amount of benthos varied with the development of the root system. The greatest quantity of benthos was found beneath *Vallisneria* which

has the most extensive root system, and the least was found beneath *Anacharis* which has a much less well developed root system.

Direct comparison of bare and vegetated areas was not made, but the data suggest that an area with a mixture of submerged aquatic vegetation would have about twice as many organisms as a non-vegetated area.

Appendix

The organisms in the Bryant's Creek Lake samples are listed to show their relative abundance on the plants and on the bottom. Animals were selected for the first list if more than 70 percent of the total number were found on the plants. The same rule was followed for the second list. The dipterous larva *Palpomyia* and the snail *Helisoma* were about equally distributed on the plants and on the bottom.

The dry weight accompanies the name of the animal if the measurement was made. The number of individuals used in the determination precedes the dash and the dry weight in g x 10^{-5} follows the dash.

The classification of Pennak (1953) has been followed.

Organisms More Abundant on Plants

Turbellaria: Planariidae

Oligochaeta: *Stylaria* (142—0.98), *Pristina, Paranais, Nais, Dero, Tubifex*

Hirudinea: *Helobdella* (6—32.0), *Piscicola*

Cladocera: *Simocephalus serrulatus* (69—5.1), *Eurycercus lammellatus*

Copepoda: Cyclopidae (14—0.36)

Amphipoda: *Hyalella azteca* (303—5.9)

Hydracarina: *Hydrachna, Diplodontus* (46—4.4), *Oxus* (29—3.5), *Limnesia* (24—5.8), *Hygrobates, Neumania, Unionicola, Albia, Geayia, Krendowskia, Arrenurus* (19—33.0)

Ephemeroptera: *Caenis* (3—6.7), *Ameletus, Pseudocloeon* (37—5.1), *Ephemerella, Cloeon, Baetis*

Odonata: *Tetragoneuria* (27—3.0), *Libellula, Anomalagrion, Ischnura, Epicordulia, Basiaeschna junata*

Hemiptera: Hebridae, *Ranatra* (1—4100.0), *Rheumobates* (6—20.0), *Trepobates* (3—23.0)

Trichoptera: *Orthotrichia* (19—3.2), *Oxythira* (82—1.1), *Polycentropus* (20—9.0), *Trianodes tarda, Trianodes injusta, Leptocella albida* (18—11.0), *Leptocella pavida, Oecetis inconspicuua* (28—1.8)

Lepidoptera: *Nymphula*

Coleptera: *Haliplus triopsis, Berosus, Laccophilus*

Diptera: *Hematopoda,* Tendipedidae (5481—5.8), *Limnophora, Culicidae, Palpomyia* (151—1.9)

Mollusca: *Helisoma* (164—3.0), *Gyraulus* (908—5.8), *Ferrissia, Sphaerium* (28—2.9)

Organisms More Abundant on the Bottom

Nematoda (46—0.87)

Annelida: *Naidium, Limnodrilus* (238—8.4), *Lumbricus* (9—620.0)

Diptera: *Chrysops* (43—28.0), *Palpomyia*

Mollusca: *Physa* (29—7.6), *Pisidium* (28—2.9), *Helisoma*

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THE MEASUREMENT OF PARTIAL INTERSPECIFIC ASSOCIATION

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INTRODUCTION

In 1949 the author proposed (Cole 1949) that the amount of association between two species should be determined from their frequency of co-occurrence in a series of samples, observations, or collections and should be expressed on a linear scale extending from zero (representing "expected" random association) to ± unity, representing the maximum possible association, positive or negative, which could have been obtained with the given series of collections. The appropriate formulas for such a "coefficient of association" were given in that paper.

Since that time a number of writers have employed this method for measuring how strongly two species are associated (*e.g.* Bray 1956; Caswell 1956; Evans and Freeman 1950; Hale 1955) and the writer has received numerous inquiries about possible applications of the method to taxonomy and other fields. Two questions have, apparently occurred to everyone who has measured or has considered measuring association in this way. First, there is the question as to how the measure of association will be affected if two somewhat different series of collections are lumped together. Second, there is the question of deciding whether the measured association represents any actual influence of the species on each other or merely reflects the degree of similarity of the habitats selected.

Both questions are undeniably important but it is no discredit to any single numerical measurement to observe that it does not simultaneously answer three rather distinct questions. Let us say for example, that we have found that two species, *A* and *B*, are much more closely associated in our samples than can reasonably be ascribed to chance. We can set forth arguments for the following hypotheses:

1) Species *A* and *B* are attracted to each other.

2) One of the species "seeks out" the other.

3) Both species are attracted to (or avoid) some third species.

4) The species select (or avoid) similar habitats.

5) Our series of observations was heterogeneous. For example, mallard ducks and sugar-maple trees sometimes occur together. If we found them together a few times in quadrats in this country and then proceeded to add into the collection a large number of African quadrats lacking both of these species, we might succeed in building up a significant association betwen them. This example is, of course, exaggerated, but it may sometimes be very difficult to conclude that some phenomenon of this sort has not entered into one's sampling.

The ecologist naturally would like to distinguish among these possibilities but no single numerical criterion, coefficient of correlation, or of association, or of anything else, computed from a heterogeneous series of collections, will do so. A more detailed analysis is necessary.

It has also been suggested that the measure of interspecific association should be extended from the case of two species to the case of *N* species, making it some sort of measure of "communality" which will enable one to judge the similarity of two communities in terms of species composition. If one will reflect that from just four species he can select six groups of two species, four groups of three species, and a group of four, the impracticality of this approach becomes evident. Suppose that species *A* and *B* are attracted to each other when *C* is present but avoid each other when *C* is absent, unless *D* is absent also! The result here might not be the same as complete independence of the four species but it would be a formid-

able task to untangle all possible such relationships for even a very small number of species.

Although there seems to be little hope for usable results in extending the measurement of interspecific association toward the measurement of communality, it does appear both worthwhile and practicable to consider the case of association among three species. To a certain extent the case of two species associated with two habitats can be treated in the same way. The analysis of this situation may make it possible to decide whether or not an observed association results from similar responses of the two species to some third species or to some recognizable environmental feature. It also raises the possibility of comparing the "strength" of an association under different conditions.

Preliminary Definitions

Given a four-fold, or "2 x 2," table of the form of Table I, the marginal totals are used to predict the values in the interior of the table on the assumption of random "scattering" of the two species relative to each other. Thus we have for the predicted values:

$$\hat{a} = \frac{(a+b)(a+c)}{N}, \hat{b} = \frac{(a+b)(b+d)}{N},$$

$$\hat{c} = \frac{(a+c)(c+d)}{N}, \text{ and } \hat{d} = \frac{(b+d)(c+d)}{N}$$

The marginal totals are accepted as strictly correct for the collections being studied, hence it is regarded as impossible that the two species could here have occurred together more times than $(a+c)$ or $(a+b)$, whichever is the smaller number.

Table I

		B: +	B: −	
Species A	+	a	b	$a+b$
	−	c	d	$c+d$
		$a+c$	$b+d$	N

In such a table the number of joint occurrences of the two species is given by a, and we define a deviation from chance association as:

$$\delta_{AB} = a - \hat{a} = a - \frac{(a+b)(a+c)}{N} = \frac{ad - bc}{N} \qquad (1)$$

It is obvious from this table that when a is increased by one unit, d must also increase by one unit, and b and c must each be decreased by unity if the marginal totals are to remain constant. Hence the largest possible value of a in any given table is governed by the size of b or c, whichever is least. For brevity in what is to follow, we define:

z_1 = either a or d, whichever is smaller.
z_2 = either b or c, whichever is smaller.

Then for a positive association ($\delta_{AB} > 0$), we may write the coefficient of interspecific association as:

$$\mathbf{C}_{AB} = \frac{\delta_{AB}}{z_2 + \delta_{AB}} \qquad (2),$$

and, for a negative association ($\delta_{AB} < 0$), the coefficient becomes:

$$\mathbf{C}_{AB} = \frac{\delta_{AB}}{z_1 - \delta_{AB}} \qquad (3).$$

The subscripts are here introduced to indicate that a table of species A vs. species B was used to compute these particular quantities. This coefficient shows what proportion of the association possible with this series of collections was actually found. **C** takes the value zero when the number of joint occurrences is exactly the expected number, it takes the value $+1$ when the species occur together as many times as they possibly could have, and it takes the value -1 when the species occurred together the minimum number of times possible with these marginal totals. Statistical significance of **C** is easily tested either applying a χ^2 test to the table directly, there being one degree of freedom for testing the four frequencies, or a standard error may be computed. We will consider significance tests later in this paper.

Collections Separable into Two Groups

Next let us suppose that the series of collections with which we have been dealing can be separated into two series by some other criterion. Such a new dichotomy might be, for example, the presence or absence of another species, C. We then subdivide our first table into two tables as follows:

Table II

$C+$

		B: +	B: −	
A	+	a_1	b_1	a_1+b_1
	−	c_1	d_1	c_1+d_1
		a_1+c_1	b_1+d_1	$Nc+$

TABLE III

$C-$

		B		
		+	−	
A	+	a_2	b_2	$a_2 + b_2$
	−	c_2	d_2	$c_2 + d_2$
		$a_2 + c_2$	$b_2 + d_2$	Nc_-

TABLE IV

$C+$

		B		
		+	−	
A	+	130 $\hat{a}_1 = 120$	270	400
	−	50	150	200
		180	420	$Nc_+ = 600$

It is obvious that each of these tables can yield a deviation representing "partial association." From Table II we can compute $\delta_{AB \cdot C+} = \frac{a_1 d_1 - b_1 c_1}{N_{C+}}$ which represents the joint occurrence (actual minus "expected") of species A and B when C is present, and from Table III we can compute $\delta_{AB:C-}$ representing the deviation from chance co-occurrence when C is absent. It is clear that if we should find, for example, that both of the other species are strongly associated with species C but not with each other when C is absent, we might suspect that any positive association found in Table I resulted from similar responses to a third species rather than from interactions between A and B. The purpose of the present paper is to show how these "partial" associations can be expressed in terms of coefficients of association exactly comparable to those defined previously (Cole 1949; cf. formulas (2) and (3) above), and to show how the effect of habitat selection, or associations with a third species, may be isolated from the intraspecific association under study.

TABLE V

$C-$

		B		
		+	−	
A	+	40 $\hat{a}_2 = 50$	60	100
	−	160	140	300
		200	200	$Nc_- = 400$

TABLE VI

Total

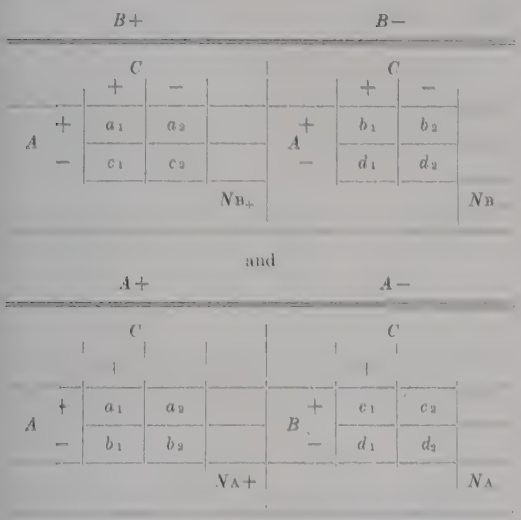
		B		
		+	−	
A	+	170 $\hat{a} = 190$	330	500
	−	210	290	500
		380	620	$N = 1000$

SUBDIVIDING THE DEVIATION-FROM-RANDOM ASSOCIATION

Perhaps the easiest way to illustrate the problem that has been bothering those working with interspecific association is to introduce a hypothetical numerical example such as that below which shows two tables of partial association and their sum, this latter being the complete series of collections.

The expected number of joint occurrences ($\hat{a}$) is shown in each table. By comparison with the "observed" it will be noted that species A and B are positively associated when C is present, negatively associated in the sub-universe $C-$, and negatively associated in the total series of collections. Also note that $\hat{a}_1 + \hat{a}_2 = 170$, but $\hat{a} = 190$ when computed from the marginal totals. Thus whether or not there is any association between the species, an "apparent" association may appear when two series of collections are combined. In fact, this result $\hat{a}_1 + \hat{a}_2 \neq \hat{a}$ is a general result unless the two marginal totals on one side of one table of partial association are in the same ratio to each other as are two of the totals on one side of the other partial table.

This "apparent" association, however, is no artifact but represents a difference in association of A and B with C, and such association is measurable. To measure all of the partial associations we would set up two more pairs of partial tables, dividing the total in two other ways. These would be:



In order to obtain the relationship between the total association and the partial associations, we proceed as follows:

We have $\delta_{AB} = (a_1 + a_2) - \frac{N_{A+} N_{B+}}{N}$,

$$\delta_{AB \cdot C+} = a_1 - \frac{(a_1 + b_1)(a_1 + c_1)}{N_{C+}},$$

and

$$\delta_{AB \cdot C-} = a_2 - \frac{(a_2 + b_2)(a_2 + c_2)}{N_{C-}}$$

We substract the partial deviations from the total and, after some algebraic manipulation, obtain:

$$\delta_{AB} = \delta_{AB \cdot C+} + \delta_{AB \cdot C-} + \frac{N}{N_{C+} N_{C-}} \delta_{AC} \delta_{BC} \quad (4).$$

This result has been obtained before (*e.g.* Yule and Kendall 1940, p. 57).

Now, the total deviation has been subdivided into three components, the two partial deviations and the term: $\frac{N}{N_{C+} N_C} \delta_{AC} \delta_{BC}$,

which represents the differential response of species A and of species B to the presence or absence of C. This is the association which would appear in Table VI as a result of adding together two sub-tables, even if each of these should show exactly the expected number of joint occurrences.

For the other two ways in which a 2 x 2 x 2 table can be subdivided one can, of course, get relationships like (4). These are:

$$\delta_{BC} = \delta_{BC \cdot A+} + \delta_{BC \cdot A-} + \frac{N}{N_{A+} N_A} \delta_{AB} \delta_{AC}, \text{ and}$$

$$\delta_{AC} = \delta_{AC \cdot B+} + \delta_{AC \cdot B-} + \frac{N}{N_{B+} N_B} \delta_{AB} \delta_{BC}. \quad (5).$$

Coefficients of Partial Association

The partial deviations we have been discussing are potentially of considerable interest to ecologists for the purpose of comparing responses of two species to each other under different conditions such as the presence or absence of a third species or of some habitat characteristic by means of which the series of collections can be separated into two groups.

To be useful for this purpose, however, it is necessary to express these partial associations in relation to the range of values that they could possibly assume. Hence, we here consider how to express these as coefficients with the same meaning as the coefficient $\mathbf{C}_{AB}$ of formulas (2) and (3). For example, the partial coefficient $\mathbf{C}_{AB \cdot C+}$ will take the value zero when the association of A and B in the presence of C is exactly what would be expected if A and B were neutral toward each other when C was present. Note that this is independent of the question of whether or not A (and/or B) responds to C; this will be shown by the values of the other partial coefficients such as $\mathbf{C}_{AC \cdot B+}$ and $\mathbf{C}_{AC \cdot B-}$. Similarly, the partial coefficients will take the values $+1$ and -1 when positive or negative association in the specified sub-universe is as strong as possible, and values between zero and unity will represent the proportion of the possible association which was actually realized.

We will again, as in discussing formulas (2) and (3), use the letters z_1 and z_2 to represent the smallest numbers in two groups. In the case of the 2 x 2 x 2 table, however, there are 8 internal numbers and there are 12 marginal totals (plus, of course, N, the total number of collections). These marginal totals we once again regard as fixed by the conditions of collecting; for example, neither species A nor B could be associated with C in more of the samples than actually contained C.

Figure 1 shows such a 2 x 2 x 2 table split into two 2 x 2 tables along one of the three possible planes in which such a division can be made. Noting that the 12 marginal totals must remain constant, we can see that for a unit increase in a_1 there must also be a unit increase in d_1 b_2, and c_2, while there must be a unit decrease in a_2, d_2, b_1, and c_1. We will here define:

$z_1 = a_1$, or d_1, or b_2, or c_2, whichever is smallest, and,

$z_2 = a_2$, or d_2, or b_1, or c_1, whichever is smallest.

We see then that the maximum possible value of a_1 for these marginal totals is $a_1 + z_2$, while the maximum possible value of a_2 is $a_2 + z_1$. Simi-

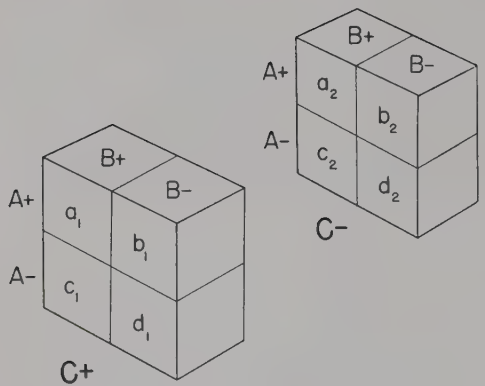


FIG. 1. A 2 X 2 X 2 table subdivided into two 2 X 2 tables.

larly, a_1 could not have been smaller than $a_1 - z_1$, nor could a_2 have been smaller than $a_2 - z_2$.

The coefficient of partial association between A and B in the sub-universe $C+$ we designate as $\mathbf{C}_{AB\cdot C+}$ and, as in formulas (2) and (3), we define the coefficient as the ratio of joint occurrences in excess of the number "expected" on the assumption of no association to the maximum possible excess (or "deficiency"). The deviation from the independent condition is given by

$$\delta_{AB\cdot C+} = a_1 - \frac{(a_1 + b_1)\,(a_1 + c_1)}{N_{C+}}$$

where N_{C+} represents the total number of samples in which C was present. If the association is positive ($\delta_{AB\cdot C+} > 0$) we obtain the coefficient by dividing $\delta_{AB\cdot C+}$ by the maximum value which it might have attained, which is simply $\delta_{AB\cdot C+} + z_2$. Thus we have:

$$\mathbf{C}_{AB\cdot C+} = \frac{\delta_{AB\cdot C+}}{z_2 + \delta_{AB\cdot C+}} \qquad (6).$$

On the other hand, if the association is negative $\delta_{AB\cdot C+}$ must be compared with the value it would have with a_1 at its minimum value of $a_1 - z_1$. Hence in this case we would have:

$$\mathbf{C}_{AB\cdot C+} = \frac{\delta_{AB\cdot C+}}{z_1 - \delta_{AB\cdot C+}} \qquad (7).$$

These coefficients of partial association are identical in form with the "total" coefficients of formulas (2) and (3). The same is true of all of the other coefficients of partial association. These results are brought together for ready reference in Table VII.

TABLE VII. Formulas for the coefficients of partial association in a 2 x 2 x 2 table

Coefficient	δ	Value when $\delta > 0$	Value when $\delta < 0$
$\mathbf{C}\ AB\cdot C+$	$\frac{a_1d_1 - b_1c_1}{N_{C+}}$	$\frac{\delta}{z_2 + \delta}$	$\frac{\delta}{z_1 - \delta}$
$\mathbf{C}\ AC\cdot B+$	$\frac{a_1c_2 - a_2c_1}{N_{B+}}$	"	"
$\mathbf{C}\ BC\cdot A+$	$\frac{a_1b_2 - a_2b_1}{N_{A+}}$	"	"
$\mathbf{C}\ AB\cdot C-$	$\frac{a_2d_2 - b_2c_2}{N_{C-}}$	$\frac{\delta}{z_1 + \delta}$	$\frac{\delta}{z_2 - \delta}$
$\mathbf{C}\ AC\cdot B-$	$\frac{b_1d_2 - b_2d_1}{N_{B-}}$	"	"
$\mathbf{C}\ BC\cdot A-$	$\frac{c_1d_2 - c_2d_1}{N_{A-}}$	"	"

THE CASE OF HABITAT SPECIFICITY

The preceding analysis has dealt with the associations among three species but the same procedure can be applied for the analysis of associations among two species and any habitat difference that is randomly sampled by the series of collections under study. If, for example, one were studying the association between two species of fleas on a series of rats he might separate the series into two parts by calling the adult rats $C+$ and the immature rats $C-$. It would then be possible to distinguish a real attraction between species A and B from an association arising from the fact that both species tend to occur more on adult rats than on immature rats.

Many cases analagous to the above will involve non-living factors of the environment. For example, a series of soil samples containing species A and B might be separable into parts by letting the dichotomy $C+$ vs. $C-$ represent samples of "wet soil" and of "dry soil." Then the association of each species with soil moisture level can be separated from any association arising from attraction or repulsion of the species for each other.

Some caution must be exercised, however, in pooled series of collections where the habitat dichotomy of interest does not enter the collections as a result of random sampling. In the example referred to above the investigator could compute a coefficient $\mathbf{C}_{AB\cdot C+}$ representing the association of species A and B in wet soil and another coefficient $\mathbf{C}_{AB\cdot C-}$ representing the association of the two species in dry soil. Now, if the investigator should make another collection of samples, this time from dry soil only, and should pool this collection with the original one he might find a new value for $\mathbf{C}_{AB\cdot C+}$, even though none of the new samples came from the sub-universe $\mathbf{C}+$! Consequently, the coefficients of partial association do not neces-

sarily give a meaningful measure of association when used in this way.

If one has a series of collections suitable for measuring the association between two species in, say, "ponds" and a comparable series from "bogs" and if he lumps these together for the purpose of computing partial associations, it will be true that the partial association $\mathbf{C}_{AB \cdot C+}$ of the species in, say, ponds may be influenced by the relative amount of collecting done in ponds and bogs. The tests of significance discussed below can be used to decide whether or not A and B are more strongly associated with each other in ponds than in bogs but the coefficients of partial association are not entirely appropriate for expressing the strength of association in such cases.

Tests of Statistical Significance

In the writer's previous paper on this subject it was proposed that a standard error derived from chi-square be attached to the coefficient of interspecific association as a ready indicator of statistical reliability. This test of significance is identical with the χ^2 test and must necessarily yield the same P values. It is, however, true, as noted by Goodall (1952), that the sampling distribution of the coefficient of association must be far from normal when the coefficient is near unity; hence the designation of a "standard error" for the coefficient is a possible source of confusion. The same problem arises in testing the significance of a correlation coefficient and is discussed by Fisher (1941, sections 33-35).

For the analysis of partial association we wish to be able to test the significance of differences between two associations, so it is necessary to examine the sampling characteristics of our statistics a little more closely.

In our 2 x 2 table (Table I) the hypothesis to be tested is that the ratio $\frac{a}{a+b}$ is equal to the ratio $\frac{c}{c+d}$ or, alternatively, that $\frac{a}{a+c} = \frac{b}{b+d}$. In words, we wish to test the hypothesis that the proportion of samples containing species A is the same when species B is present as when species B is absent (or, alternatively, that the proportion containing B is the same when A is present as when it is absent).

The probability of finding species A in any particular sample picked at random from among the N collections summarized in Table I is given by the marginal totals and is $p = (a + b)/N$. The probability that A will be absent is $q = 1 - p = (c + d)/N$. Now for the collections with B present we have a sample of size $(a + c)$ drawn from a universe with p and q as above assuming the marginal totals to be reasonably large. Consequently, the variance of the proportion of these containing A is:

$$S^2_{B+} = \frac{pq}{N_{B+}} = \frac{(a+b)(c+d)}{N^2(a+c)}.$$

Similarly, the variance in the sample lacking B is:

$$S^2_{B-} = \frac{pq}{N_{B-}} = \frac{(a+b)(c+d)}{N^2(b+d)},$$

considering the samples as independent. The variance of the difference between the two proportions is the sum of the separate variances, or:

$$S^2_{Diff.} = S^2_{B+} + S^2_{B-} = \frac{(a+b)(c+d)}{N(a+c)(b+d)} \quad (8).$$

Accordingly, the ratio, $\frac{a}{a+c} - \frac{b}{b+d}$, divided by $S_{Diff.}$ will be normally distributed with unit variance about a mean of zero. This ratio is:

$$t = (ad - bc)\sqrt{\frac{N}{(a+b)(a+c)(b+d)(c+d)}} = \sqrt{\chi^2} \quad (9).$$

Hence, either tables of the normal curve or the Chi-square test may be used for judging the significance of association in a 2 x 2 table if the marginal totals are large enough to provide a good estimate of the probability, p.

For the numerical example of Table VI we have

$$\frac{a}{a+c} - \frac{b}{b+d} = -.0849 \quad \text{and} \quad S_{Diff.} = .0326.$$

Hence this difference is 2.6 times its standard error, which corresponds to a P value of .009, considering both tails of the normal curve. We therefore consider this negative association to be statistically significant.

For testing the significance of an observed difference between two partial associations it is necessary to specify just what hypothesis is to be tested, and a number of tests can be devised corresponding to different hypotheses.

For a set of data subdivided as in Tables II and III (or as shown in Fig. 1) we will have computed two coefficients of partial association $\mathbf{C}_{AB \cdot C+}$ and $\mathbf{C}_{AB \cdot C-}$ and we may wish to decide whether or not there is a significant difference between them. The simplest approach to this problem would seem to be as follows: Regard the two tables (II and III) as independent samples from one parent universe and investigate whether the ob-

served proportions of "joint occurrences" of species A and species B can reasonably be attributed to random sampling from such a universe.

The hypothesis to be tested then, using the symbols of Tables II and III, is that $\frac{a_1}{N_{C+}} = \frac{a_2}{N_{C-}}$. For the total series of collections the probability that any single observation will represent a joint occurrence of A and B is $p = \frac{a_1 + a_2}{N}$ and the probability that this observation will not be a joint occurrence will be $q = 1 - p$.

Proceeding exactly as in the case of formula (8) then, we expect the difference $\frac{a_1}{N_{C+}} - \frac{a_2}{N_{C-}}$ to be normally distributed about zero with variance:

$$S^2_{Diff.} = \left(\frac{a_1 + a_2}{N}\right)\left(\frac{N - a_1 - a_2}{N}\right)\left(\frac{1}{N_{C+}} + \frac{1}{N_{C-}}\right) \qquad (10).$$

If we consider the numerical example of Tables IV and V we may wish to decide whether the observed difference in the association of species A and B in the two tables is to be regarded as significant. For this purpose, referring to Table VI, we estimate: $p = 17/100$ and $q = 83/100$, which gives us

$$S^2_{Diff.} = \left(\frac{17}{100}\right)\left(\frac{83}{100}\right)\left(\frac{1}{600} + \frac{1}{400}\right)$$

The observed difference in proportions of joint occurrences is $130/600 - 40/400 = 7/60$ and we have: $t = \frac{7/60}{S_{Diff.}} = 4.8$. For a normal deviate 4.8 times its standard error we obtain a P value of about 2×10^{-6} from which we conclude that there is a highly significant tendency for species A and B to be more closely associated when C is present than when it is absent.

Discussion and Summary

The present paper extends the analysis of interspecific association in what appears to be the most useful direction for ecological studies

It was pointed out by Forbes (1907) that when two species occupy the same general locality so that any collection may include either of them, we would expect some collections by chance to include both species even if they are entirely neutral toward each other. The number of such chance co-occurrences will depend upon the frequencies with which the species occur in the sampling units and, of course, we have estimates of these frequencies from the actual results of our collecting.

If the two species actually occur together more often than would be expected by chance we regard the excess number of co-occurrences, here called δ, as a measure of association between the two species. The coefficient of interspecific association described earlier by the writer merely expresses the observed δ as a proportion of the maximum value possible with the observed frequencies of the two species. The same description applies, of course, to negative association. This measure then provides a convenient way of indicating the strength of an association, and the statistical reliability of the measure is easily determined.

The present paper extends this analysis from the case of two species to the case of three species taken two at a time, although the third "species" may under many conditions just as well represent the presence or absence of some non-living habitat feature. In this case, instead of analyzing a single 2 x 2 table, we put two such tables together to make a cubic 2 x 2 x 2 table. This cubic table may then be taken apart again along any of three planes so that we can compare and test for statistical significance three sets of coefficients of partial association which take the same arithmetic form and are subject to the same interpretations as the coefficients of association described previously.

In such a 2 x 2 x 2 table the marginal totals (collection results) can be used to obtain four distinct "expected" values for any of the eight internal numbers representing joint occurrences. Thus for our analysis we compute an "expected" value for a_1 of Figure 1 in three ways; on the assumption that A and C are independent, on the assumption that A and B are independent, and on the assumption that B and C are independent. We could obtain a fourth value by assuming that A, B, and C are all independent, but this value appears to be of little interest for the purpose at hand. It is quite possible for this "expected" value to agree exactly with the observed number of collections yielding all three species and yet to have strong association among the species considered in pairs. Thus, any coefficient of "manifold" association computed from such a table could be very misleading. A meaningful measure of such "manifold" association is apparently what some ecologists would like to have as a measure of "communality" but the writer considers that no such measure is possible.

Even in the case of a 2 x 2 x 2 table, a cube representing the interrelations of three species, there are several distinct ways of having pairs of

species react toward each other to yield the same result in terms of "triple" association. For our hypothetical example of Tables IV, V, and VI, a_1 (= 130), is greater than $\frac{N_{A+}\, N_{B+}\, N_{C+}}{N^2}$ (= 114), its "expected" value on the assumption that the three species are completely independent. The "triple" association would, therefore, be judged as positive. This, however, does not provide evidence of "communality" or of any tendency for the three species to be drawn together as a group. Actually, in this case the association between B and C is always negative ($\mathbf{C}_{BC} = -.21$, $\mathbf{C}_{BC\cdot A+} = -.09$, and $\mathbf{C}_{BC\cdot A-} = -.36$) but this is offset in the "manifold" association by a positive association between A and C, and by the tendency for A and B to be positively associated when C is present. In the hypercubes that would have to be analyzed when considering more than three species the possibilities for erroneous interpretation of "manifold" association would be tremendously increased.

The approach through "partial association," however, does open possibilities for distinguishing between actual interaction between species and the effects of habitat specificity, or responses of two "neutral" species to some third species.

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THE DYNAMICS OF THREE NATURAL POPULATIONS OF THE DEER *ODOCOILEUS HEMIONUS COLUMBIANUS*[1]

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Introduction

In the course of an investigation of the ecology of the Columbian black-tailed deer (*Odocoileus hemionus columbianus* (Richardson), in relation to chaparral management in Lake County, California, information on the dynamics of three natural populations has been obtained. These populations occupy different habitats. The original plant community and environment were common to all, but secondary modification has created three distinct range types.

The climax plant cover consists on south slopes of *chamise chaparral* and on the north slopes of *broad sclerophyll forest* as described by Cooper (1922). These associations are dominated by fire-tolerant shrubs which either sprout from the root-crown when burned or have seeds which germinate readily following heating.

On the southerly exposures the most abundant plant is chamise (*Adenostema fasciculatum*). Other species include yerba santa (*Eriodictyon californicum*), wedgeleaf ceanothus (*Ceanothus cuneatus*), and toyon (*Photinia arbutifolia*). Occasional burning apparently took place on these slopes during prehistoric times.

The northerly exposures were largely covered, before white settlement, with a broad-sclerophyll forest, in which the dominant trees were interior live-oak (*Quercus wislizenii*), canyon oak (*Q. chrysolepis*), California laurel (*Umbellularia californica*) and madrone (*Arbutus menziesii*). Since that time (1855-65) fires have become more frequent and at present much of the north-exposure vegetation must be called mixed or mesic chaparral, consisting of broad-sclerophyll species which have been reduced to shrub form by burning. The principal constituent of this association is interior live oak (*Quercus wislizenii*). A large assemblage of other woody plants including scrub oak (*Q. dumosa*), Eastwood manzanita (*Arctostaphylos glandulosa*), and deerbrush (*Ceanothus*

[1] Contribution from Federal Aid in Wildlife Restoration Project California W-31-R and the Museum of Vertebrate Zoology, University of California.

integerrimus) is also found on north exposures.

At present the general cycle of events is that every five to twenty years or more a fire sweeps the region bare, except for isolated patches of brush and the bare, charred trunks of the burned shrubs. Within five to ten years the sprouts and seedlings have grown up to cover the ground with a dense thicket of shrubs. Two of the range-types that were compared in this study are the two extremes of this burn-and-recover pattern: the newly burned area on which crown-sprouts and seedlings are abundant—here called the "wildfire burn"; and the area which has not been burned for at least 10 years—here called the "chaparral." The wildfire burn is admittedly a transient stage, but while it lasts it constitutes a special type of deer range, being rich in food and poor in cover.

Another modification of chaparral is possible. Certain portions may be burned deliberately in either the early spring or late summer, and the burned areas seeded to herbaceous species. After the rains, when the seedlings emerge, those of the herbaceous species compete successfully with those of the woody species. The brush-sprouts are kept hedged by deer use or reduced by re-burning. The net result is a scattering of shrubs with the intervening area occupied by herbaceous plants. When an area is managed in this way portions are left in heavy brush for cover. This range type is now called "shrubland."

The technique of managing chaparral to create shrubland is still in the experimental stage so the areas of shrubland are limited in extent. The area most intensively studied covered about 400 map acres (horizontal projection) and was followed from before burning, in 1949, until 1955. Areas which had been longer established were also studied.

Some discussion of the ecology of these chaparral cover types has been included in a previous publication (Biswell *et al.* 1952), and a fuller description of the plant cover, with special reference to use by deer, will form the body of a later report.

The three range-types under consideration may occur in close juxtaposition, and it was in such an area that the present studies were made. The area lies about five miles southwest of Lakeport, California, between the elevations of 1500 and 2500 feet. The substrate consists of Pliocene sandstones elevated in Pleistocene times (Manning and Ogle 1950). Erosion has been rapid and the soils are correspondingly thin. They are classified principally as *Maymen,* with lesser areas of *Los Gatos.* Small pockets of still other residual soils occur on the uplands, and alluvial soils are found in the stream-bottoms. The topography is moderately steep (average slope = 22 degrees), and consists of irregular drainages and ridges with rounded tops. Rainfall averages about 28 inches annually. Winter snows usually melt soon after they fall, especially on the warmer south exposures where the deer spend most of their time in winter.

The adjustment of the vegetation to the Mediterranean climate has a profound effect upon the food-regime of the deer. Most of the shrubs are evergreen, but do not grow in the winter, when it is moist enough but too cold, or in the summer, when it is warm enough but too dry. Ordinarily there is some growth in crown-sprouts in late fall, but little or none in mature shrubs. The principal growth period, then, is spring. In April and May, the deer, feeding on the new shoots, gain weight rapidly. Most fawns are born in the second and third weeks of May. The last rains usually fall in May. Increasing drought dries the herbaceous plants and the shrubs become dormant in July. The moisture and crude protein levels in the browse fall steadily all summer, and the condition of the deer, especially lactating does, falls accordingly. Occasionally there is a heavy set of acorns and the deer begin to browse these directly from the low oaks in August and September, months when otherwise the forage is of low quality. In the fall come cool weather and the first rains. The timing of the first substantial rain is especially important in the shrubland, where large quantities of annual plants appear if about one inch of rain falls. Sufficient rain for germination usually falls in October, but occasionally the first heavy precipitation may be as early as August or as late as November.

The present study began in the fall of 1948 and continued through the fall of 1955. Many people aided the investigation: of the field forces of the California Department of Fish and Game, Norman Alstot, Gordon Ashcraft, Bonar Blong, Herbert Hagen and Manley Inlay; of the State Fish and Game Laboratory, John Azevedo, Art Bischoff, Oscar Brunetti and Merton Rosen. Help in the field was also provided by Richard Genelly and Gerald Geraldson of the University of California. Aid, advice, and encouragement were constantly available from H. H. Biswell, Project Leader, A. M. Schultz, A. S. Leopold and W. M. Longhurst, of the University of California, and William Dasmann and Robert Lassen of the Department of Fish and Game. To these, and to Glen Keithley and Harold Manley on whose land much of the work was done, and to others too numerous to list, we are indebted for help.

In addition we wish to acknowledge the critical reading of the manuscript, with suggestions for improvement, by W. Leslie Robinette, J. J. Hickey, Robert F. Scott and staff members of the Museum of Vertebrate Zoology.

Methods and Results

The basic data from which the life tables were derived consist of information on individual movement, population density, reproduction according to age-class, populaton structure, and mortality according to age and sex. These data were gathered seasonally for the three populations under study; notes on the methods involved are given below.

Movement

By studying the movements of marked deer daily, seasonally and annually, it has been found that the deer in the study region are nonmigratory and that most of them occupy home ranges with diameters of about one-half mile (does) to three-quarters of a mile (bucks). Populations occupying neighboring ranges may, therefore, be considered separately (Dasmann 1953).

Population density

Censuses were made at least twice a year, first by the pellet-group-count method and later by the sample-area-count method, both of which were found to be accurate when checked against populations of known density. These methods are described elsewhere (Dasmann and Taber 1955).

Table I shows population densities observed at various times on the three types of range under study. Counts in the chaparral gave a summer density of about 30 per square mile. The wildfire burn, at the same season, showed 120 the first year after the fire. The summer density dropped to 106 the second year, 52 the third and 44 the fourth. The shrubland went from 98 the year following burning to 131 the second year and then down to about 84 the fifth and sixth years, at which level the population presumably stabilized.

Natality

Data on ovulation rates were obtained by collecting pregnant and post-partum does. Forty-eight does over 17 months of age were taken on the three range types. Younger does were also collected and were found not to breed under our conditions (Taber 1952).

The presence of *corpora lutea of pregnancy* is an indicator of the successful shedding, fertilization and implanation of ova, but not every *corpus luteum* represents a developing fetus. The ratio

Table I. Deer density (individuals per map-square-mile) on three range-types

A. Chaparral

	April-June	July-October	November-December
1949	28	..	30
1950	13	30	26
1951	..	..	30
Average.....	20	..	29

B. Wildfire burn

Growing season from time of burning	Early May	Mid-July	Early December
1	..	120	86
2	75	106	56
3	48	52	50
4	32	44	32

C. Shrubland

	Early May	Mid-July	Early December
1951	88	131	88
1952	69	112	99
1953	69	103	..
1954	53	85*	..
1955	55	82*	..

*mid-June.

was found to be 94 fetuses per 100 corpora lutea, based on all pregnant does collected. No evidence of abortion or resorption was noted, so this six per cent loss of ova must occur before fertilization or in very early pregnancy.

Does often breed first, in this region, at the age of 17 months, although on the poorer ranges some may not breed until the age of 29 or even 41 months. No yearling does (17-24 months) were collected in the poorest range type, the chaparral. Two from the shrubland had one fetus apiece and two out of three from the new wildfire burn had one fetus each. Two yearling does were taken from an older wildfire burn and neither was pregnant. These samples are so small that little confidence can be placed in them. However, some values for the contribution of yearling does to the annual fawn-increment must be assumed in the calculations which follow, so these figures for the shrubland and new wildfire burn will tentatively be accepted. In addition, since no data are available for reproduction in yearling does in the chaparral, it will be assumed that the rate of fawn production by them is 0.5 per doe.

Among adult does the samples are larger, ranging for the three range types from 10 to 16. Fawn

TABLE II. Fawn production by yearling and adult does on three range types

Range type	Yearling Does			Adult Does		
	Number examined	Mean number of corpora lutea	Fawns produced per doe	Number examined	†Mean number of corpora lutea	Fawns produced per doe
Chaparral	0	....	*0.50	11	0.82 (0.42 - 1.22)	0.77
Wildfire burn after one growing season	3	0.66	0.62	10	1.40 (1.03 - 1.77)	1.32
Wildfire burn after three growing seasons	2	0.0	0.0	4	0.75 (0.00 - 1.54)	0.71
Shrubland	2	1.0	0.94	16	1.75 (1.51 - 1.99)	1.65

*Assumed (see text).
†Values in parentheses indicate the range with a confidence limit = .05.

production in the shrubland is significantly higher than that in the chaparral, the values being 1.65 and 0.77 fawns per doe respectively. The does on the new wildfire burn show an intermediate average of 1.32 fawns apiece. Fawn production is summarized in Table II.

Population structure

Population structure was determined by observing and classifying undisturbed deer at ranges consistent with accuracy, at times during which all age and sex classes were equally visible. The most favorable seasons were late July, when fawns were at heel and before hot weather caused the bucks to seek heavy cover, and early December, when the rut had subsided and the bucks had returned to their normal level of mobility but before the antlers were shed (Dasmann and Taber 1956). In shrubland, where a more intensive study was carried out, determinations were made throughout the year. The values in Table III are expressed in terms of ratios, where the number of adult does is always taken as 100.

The low density of deer and the high density of cover made herd composition counts difficult to obtain in the chaparral. Therefore use was made of the fact that when an area of chaparral is burned, and sprouts appear, as happened in 1949 and 1950, the deer whose home ranges impinge upon the burned area congregate on it to feed and are then (December) easily observed. This population may be taken to represent the population in the chaparral, so far as structure is concerned, if one correction is made. Since the home ranges of bucks are larger than those of does, a burned area attracts proportionally more bucks than does, if only those animals whose home ranges impinge upon the burned area come to it. The counts in Table III(A) are corrected for this; i.e. adult buck counts were reduced one-third, because average buck home-range diameter is ⅔ average doe home-range diameter.

TABLE III. Population structure according to herd composition counts on three range types

Month	Number of deer classified	Adult ♂ ♂	Yearling ♂ ♂	Adult ♀ ♀	Yearling ♀ ♀	Fawns
A. Chaparral						
Dec. 1949	124	72	23	100	38	85
Dec. 1950	47	20	5	100	25	60
Average	85	46	14	100	31	72
B. Wildfire burn (December counts)						
During growing season						
1 (1948 burn) counted in 1949	90	63	30	100	33	107
4 (1948 burn) counted in 1952	37	50	14	100	21	79
1 (1950 burn)	54	37	21	100	39	89
2 "	45	66	20	100	33	80
3 "	90	48	7	100	27	34
C. Shrubland						
July, 1951	82	70	27	100	46	127
Dec., 1951	55	30	30	100	45	70
May, 1952	43	38	31	100	44	56
July, 1952	70	48	9	100	30	117
Dec., 1952	62	39	9	100	30	92
May, 1953	43	32	9	100	14	41
June, 1953	67	36	16	100	20	96
May, 1954	33	39	29	100	14	57
June, 1954	53	56	25	100	25	125
May, 1955	34	46	31	100	8	77
June, 1955	51	71	36	100	36	121

Mortality

Every carcass encountered was classified, if possible, according to age, sex, season of death, cause of death and range type. Occasionally special systematic searches were made for carcasses, especially along the beds of steep-walled canyons, where dead deer were most likely to accumulate. Altogether 222 carcasses were tallied; these are listed in Table IV. Aging was by tooth eruption and wear (Severinghaus 1949; Moreland 1952).

A carcass-count of this sort is not a true re-

TABLE IV. The classification of deer found dead on three range types

Sex	0 - 3 months	4 - 6 months	7 - 9 months	10 - 12 months	13 - 24 months	25 - 36 months	37 months and over	Total
A. Chaparral								
♂	0	7	6	0	8	3	9	33
♀	1	6	4	0	1	1	23	36
?	16	0	0	0	0	0	0	16
							Sub-total.....	85
B. Wildfire burn—one to four years after burning								
♂	7	1	2	0	1	6	12	29
♀	1	4	1	0	1	1	11	19
?	16	0	0	0	0	0	0	16
							Sub-total.....	64
C. Shrubland								
♂	3	7	1	2	5	4	4	26
♀	1	5	0	0	0	4	18	28
?	19	0	0	0	0	0	0	19
							Sub-total.....	73
							Grand total.....	222

flection of mortality in all classes; the very young deer are under-represented, because their fragile carcasses soon disintegrate. However, if this is taken into account, the carcass tally aids the study of mortality.

The principal cause of mortality was starvation, not caused by a quantitative lack of food, but rather by a seasonal drop in the quality of available forage (Taber 1956). The effects of starvation were often augmented by exposure to unfavorable weather and occasionally by disease or parasitism. Mortality from this cause was heaviest among fawns, but adults of both sexes were also affected. Principal starvation losses occurred in fall and winter. Next in importance as a mortality factor was hunting. Almost all adult buck mortality, except for old deer, was caused by bullet-wounds. A few deer of other classes were also affected. The loss of protected classes to hunting varies widely. It was found in the study region to be quite low. A few deer were killed in accidents or by predators, but these are relatively unimportant mortality factors.

The hunting season extends from early August to mid-September and bucks usually become legal game during their third year and remain so for the rest of their lives. The kill at this time has a profound effect on the population structure. The ratios existing between two-year, three-year and older bucks in the kill, which are given in Table V, are affected by three factors: the age distribution of bucks in the population; the relative vulnerability of the various age classes to hunting; and the deliberate selection of the larger (hence older) bucks by the hunter.

Where hunting pressure is only moderate and

TABLE V. Distribution by age (in per cent) of bucks killed and taken home from three range types

Range type	Two years old	Three years old	Four years old and older	Number in sample
Chaparral.....	40	22	38	194
Wildfire burn after first growing season.....	36	22	*42	59
After second growing season.....	63	21	15	52
After third growing season.....	37	37	25	83
After fourth growing season.....	50	22	28	32
Shrubland.....	49	19	32	43

*Old bucks are unusually vulnerable during the first hunting season after a large wildfire has removed most of the escape cover.

escape cover is adequate, bucks over four years old are much less vulnerable than two-year-olds, with three-year-olds being intermediate. For example: in an intensively studied area of shrubland the combined buck populations for the seasons of 1951 and 1952 were 14 two-year-olds, of which 10 were killed, and 13 older bucks, of which two were killed. This difference in vulnerability is probably above the average because little drive-hunting with dogs took place. This type of hunting results in a proportionally higher kill of old bucks.

Selective hunting, involving the deliberate attempt of the hunter to bag a trophy buck, is generally not practiced. Most hunters attempt to take the first legal target that they see. If the antlers are small and inconspicuous the hunter may not recognize the deer as legal game, or if two bucks appear together, the hunter will select the larger, but these factors do not appear to affect the kill appreciably. These remarks apply to hunters on public land, and private land with public access. All the areas studied except part of the shrubland could be so classed. However, there are certain lightly hunted areas of private land where there is a definite selection of larger (hence older) bucks by the hunter. Part of the shrubland of the present study was in this category, and for that reason the percent of old bucks in the kill (Table V) is believed to be higher than would ordinarily be found.

In addition to the bucks which are killed and taken home by the hunters, there are those which are shot but not found. In the study region hunters often shoot across canyons at running deer at long range. This fact, and the heavy cover and the hard ground, which makes tracking difficult, lead to the loss of many wounded deer. Few of these recover. Intensive studies of small known populations have shown this loss to equal about 40 per cent, or slightly more, of the take-home kill.

TABLE VI. The population dynamics, through one year, of a deer population inhabiting 100 square miles of chaparral

Season	4+ yr. ♂♂	3 yr. ♂♂	2 yr. ♂♂	1 yr. ♂♂	3+ yr. ♀♀	2 yr. ♀♀	1 yr. ♀♀	♂Fawns	♀Fawns	Total
Late May (fawn drop)	343	121	190	239	1063	262	280	504	446	3448
Early summer loss	...	...	...	...	...	...	...	180	114	294
July herd composition count	343	121	190	239	1063	262	280	324	332	3154
Hunting season bag	39	27	49	...	...	...	...	...	...	115
Crippling loss	16	11	20	...	...	...	...	...	...	47
Late summer and fall loss	...	...	...	43	152	17	8	31	19	270
Dec. herd composition count	288	83	121	196	911	245	272	293	313	2722
Late winter loss	28	...	...	6	80	13	10	54	33	224
Early May population	260	83	121	190	831	232	262	239	280	2498
Late May (fawn drop)	343↙	121↙	190↙	239↙	1063↙	262↙	280↙	504	446	3448

RECONSTRUCTION OF POPULATION DYNAMICS

The information presented above has been used to deduce the detailed changes taking place within each population in the course of a year or, in the wildfire burn population, four years. In order that values per square mile may be readily derived, the tables of population dynamics given in this section are constructed to represent the deer population occupying 100 square miles of the range-type in question. In a later section, where life tables are presented, values in per cent may be more readily apprehended.

Annual population cycle: chaparral

From data presented above it may be seen that the deer population in the chaparral is one of low density, with a low reproductive rate. Since the population is stable, this low reproductive rate is matched by a relatively low mortality. Does probably do not breed as early as they do on better ranges, and they certainly do not bear as many fawns in maturity. It is possible that some individuals bred only in alternate years. This partly relieves the population of the heaviest drain on adult vitality—gestation and especially lactation, where lactation takes place at a season of a falling nutritive plane. Mortality among fawns, though high, is not as high proportionately as it is on also fully stocked but better ranges, like shrubland. Presumably this is due in some measure to the fact that most fawns are born singly. Mortality among bucks during the hunting season is lighter than in more open range because the abundance of dense escape cover in the chaparral makes hunting difficult. The general pattern is of a population with a rather low rate of replacement and a correspondingly high life expectancy from adulthood. An annual cycle is shown in Table VI.

Annual population cycle: wildfire burn

The general trend of population density characteristic of wildfire burns is from a high point the spring following burning to lower and lower levels thereafter. Movement is the most important element in these population changes.

When the area burns the deer move ahead of the fire and are seldom directly injured. Lack of food, however, keeps them from re-occupying their home ranges, unless there happens to have been a heavy acorn crop. The brush on the warmer slopes sprouts from the root-crown about October or November, in areas burned in late summer. The wildfire burn thereupon becomes an attractive feeding area, and large numbers of deer appear on it. The deer densities observed on burned areas can be adequately explained by supposing that the deer feeding on the burned area are those whose home ranges included part of that area before it was burned. If this is true, deer are drawn to a burned area from a peripheral zone one-half mile wide for does and three-quarters of a mile wide for bucks; *i.e.*—the peripheral zone equals one home-range diameter in width. Thus if burns are small the deer density feeding upon them is high, whereas if burns are large the density is lower, because in the former case the peripheral zone is larger in proportion to the burned area and in the latter it is smaller.

Actual observations of increase in deer density following burning correspond, for the areas representative of wildfire burns, to that to be expected if a strip one-half mile in width were burned through the country. Therefore in the reconstruction of population dynamics (Table VII) it has been assumed that the burn consists of a strip one-half mile in width extending indefinitely across the country, and the population shown is that inhabiting 100 square miles of this burn.

In order to follow the dynamics of a deer population through four years, as has been attempted in Table VII, it is necessary to use some interpolated values for productivity. It has been seen (Table II) that the average fawn production per doe in

TABLE VII. Dynamics of a deer population inhabiting 100 square miles of wildfire burn for the first four years following burning

Season	4+ yr. ♂♂	3 yr. ♂♂	2 yr. ♂♂	1 yr. ♂♂	3+ yr. ♀♀	2 yr. ♀♀	1 yr. ♀♀	♂Fawns	♀Fawns	Total
Original population (Dec.)	406	83	99	196	740	344	362	276	395	2901
Influx from periphery	406	83	225	444	1247	580	610	695	1003	5293
Early May population	812	166	324	640	1987	924	972	971	1398	8194
Fawn-drop	978	324	640	971	2911	972	1398	2098	1856	12148
Early summer loss	...	...	...	...	...	...	...	92	56	148
July herd composition count	978	324	640	971	2911	972	1398	2006	1800	12000
Hunting bag	126	66	108	...	...	...	...	...	...	300
Crippling loss	50	26	43	...	...	...	...	...	...	119
Late summer and fall loss	...	...	...	...	...	...	...	100	61	161
Exodus	145	42	107	175	799	267	377	524	478	2914
Dec. herd composition count	657	190	382	796	2112	705	1021	1382	1261	8506
Exodus	46	11	29	48	117	39	57	77	70	494
Late winter loss	...	...	...	...	7	...	...	473	106	586
Early May population	611	179	353	748	1988	666	964	832	1085	7426
Fawn-drop	790	353	748	832	2654	964	1085	2176	1925	11527
Early summer loss	...	...	...	...	...	...	...	589	437	1026
July herd composition count	790	353	748	832	2654	964	1085	1587	1488	10501
Hunting bag	66	92	277	...	...	...	...	...	...	435
Crippling loss	26	37	111	...	...	...	...	...	...	174
Late summer and fall loss	...	...	...	...	...	...	...	279	133	412
Exodus	259	69	55	386	1062	386	434	635	595	3881
Dec. herd composition count	439	155	305	446	1592	578	651	673	760	5599
Exodus	114	...	...	196	400	150	169	175	198	1402
Late winter loss	35	...	...	...	152	...	...	218	42	447
Early May population	290	155	305	250	1040	428	482	280	520	3750
Fawn-drop	445	305	250	280	1468	482	520	1067	943	5760
Early summer loss	...	...	...	...	...	...	...	380	230	610
July herd composition count	445	305	250	280	1468	482	520	687	713	5150
Hunting bag	64	93	93	...	...	...	...	...	...	250
Crippling loss	26	37	37	...	...	...	...	...	...	100
Late summer and fall loss	...	...	...	...	18	...	...	165	101	284
Dec. herd composition count	355	175	120	280	1450	482	520	522	612	4516
Late winter loss	94	...	...	...	646	...	...	336	204	1280
Early May population	261	175	120	280	804	482	520	186	408	3236
Fawn-drop	436	120	280	186	1286	520	408	822	727	4785
Early summer loss	...	...	...	...	...	...	...	261	174	435
July herd composition count	436	120	280	186	1286	520	408	561	553	4350
Hunting bag	44	34	104	...	...	...	...	...	...	182
Crippling loss	18	14	42	...	...	...	...	...	...	74
Late summer and fall loss	...	...	...	33	307	10	10	210	140	710
Dec. herd composition count	374	72	134	153	979	510	398	351	413	3384

the new wildfire burn is about 0.62 for yearlings and 1.32 for adults. As the wildfire burn grows older the quality of the forage produced on it drops, and this is reflected in the reproductive rate. By the fourth year after burning reproduction appears, according to evidence from limited collecting and herd composition counts, to be about the same as that in the heavy brush, namely 0.5 fawns per yearling doe and 0.77 fawns per adult doe. It remains to interpolate intermediate values for productivity during the second and third years following burning. We will assume that yearling does each produce an average of 0.58 and 0.54 fawns and adult does 1.14 and 0.95 during the second and third years following burning, respectively.

Table VII traces the dynamics of a deer population inhabiting a wildfire burn from the December following burning for four full years. The population, if there had been no fire, would have been about 29 per square mile. The influx of deer whose home ranges abutted on the burned area added another 53 per square mile. These deer, which bred in early November, showed a reproductive rate somewhat greater than that found in the chaparral. Presumably this was due either to a high-quality diet of new sprouts for a few weeks prior to breeding, or to the psychic stimulation of crowding in the periphery of the burn during the rut. The former seems more probable.

With the onset of cold weather there was apparently an exodus of a portion of the population from the burned area, where there was little heavy cover, to the periphery, and these did not return. There was apparently a similar movement the following winter. In both cases the population

TABLE VIII. Dynamics of a deer population inhabiting 100 square miles of shrubland

Season	4+ yr. ♂♂	3 yr. ♂♂	2 yr. ♂♂	1 yr. ♂♂	3+ yr. ♀♀	2 yr. ♀♀	1 yr. ♀♀	Fawns ♂♂	Fawns ♀♀	Total
Late May (fawn-drop)	434	182	482	556	1935	706	858	2042	1810	9005
Early summer loss	...	...	...	...	29	...	...	350	224	603
July herd composition count	434	182	482	556	1906	706	858	1692	1586	8402
Hunting season bag	60	46	214	...	...	...	...	...	...	320
Crippling loss	24	19	86	...	...	...	...	...	...	129
Late summer and fall loss	...	...	...	20	115	37	20	856	547	1595
Dec. herd composition count	350	117	182	536	1791	669	838	836	1039	6358
Late winter loss	33	...	...	54	414	111	132	280	181	1205
Early May population	317	117	182	482	1377	558	706	556	858	5154
Late May (fawn-drop)	434	182	482	556	1935	706	858	2042	1810	9005

dropped but a lack of carcasses indicated that movement rather than mortality was the cause.

Mortality on new wildfire burns was found to be very low, as might be expected from the high quality of the feed there. However, as forage quality declined, mortality increased.

By the end of the fourth year the deer population in the wildfire burn had declined to about the levels in the chaparral both in density and reproduction.

Annual population cycle: shrubland

The management of chaparral to create shrubland resulted in the attraction of a heavy deer population, in much the same manner as has been described for the wildfire burn. There were, however, several important points of difference between the shrubland and the wildfire burn. In the shrubland there were areas of cover closely adjacent to feeding grounds; the wildfire burn had little cover. In the shrubland there was an abundance of herbaceous forage, which the deer eat in quantity from December through March; in the wildfire burn there was little herbaceous forage. In the shrubland the browsing-pressure of the deer was sufficient to keep many shrubs hedged and within reach; the browsing pressure on the wildfire burn was not usually sufficient for this and shrubs tended to grow beyond reach. Because of these, and perhaps other factors, the shrubland continued to support a high deer density throughout the study. This density was very high during the first years due to influx and a high survival. By the fifth and sixth year following burning, however, it had stabilized at a lower, but still substantial density. It appears that this level, about 84 per square mile in July, can be maintained for some time, so it has been taken as the basis for the annual cycle of population dynamics reconstructed in Table VIII.

The shrubland range is fully stocked and population gain is matched by loss. The reproductive rate is high. Most yearling does produce a fawn and adult does produce an average of 1.65 fawns apiece. The mortality in these fawns is high; during the first year of life 73 per cent of the males and 53 per cent of the females die. Among adult does mortality is also high—about 25 per cent per year. Adult bucks, because of heavy hunting and the prevalence of open country, lost 62 per cent of two-year-olds, 35 percent of three-year-olds and about 20 per cent of older bucks to hunting, on the average.

Among yearling (12- to 24-month-old) deer not all the loss to the population was due to mortality. It is usual for a dispersal movement of yearlings to occur about fawning-time, when the adult does become antagonistic toward their previous offspring. In a large, homogeneous area, of uniform deer density, this movement of yearlings from a local area would be balanced by others moving into it. A small area of dense population, however, would tend to lose more than it gained; this is the situation on the 400-acre shrubland study area. Here the average loss due to emigration during the four year period 1951-55 amounted to about 6 per cent of the yearling class of bucks and 38 per cent of the yearling class of does. It seems probable that this higher emigration rate in yearling females is connected with the tendency toward spacing and mutual antagonism among breeding does (Dasmann and Taber 1956).

Since this measurement of emigration was made on a small area of dense population, it is large. In Table VIII, which is an attempt to describe shrubland population dynamics for a larger area, a yearling female emigration of 15 per cent is assumed.

Life tables for wild ungulates

It has been apparent, in preceding sections, that in any of the populations under study the dynamics of the male portion of the population differed from that of the female portion. This was due partly to a differential mortality in early life and partly to the fact that when adulthood was

reached entirely different decimating factors were at work—physiological reproductive drain, coupled with reduced nutrient quality, for females, and predation (in the form of hunting) for males. In other populations it is probable that still other factors might be operative. As an analytical aid, then, it seems proper to consider the male and female components of each population separately.

The life table, as so ably described and used by Deevey (1947) and Hickey (1952) is a convenient vehicle for describing a population so that certain characteristics can be readily ascertained. The data, or values derived from them, are cast under the headings: x—the age-interval, in our case one year; l_x—the number alive at the beginning of each year; d_x—the number dying within the year; q_x—the rate of mortality during the year ($100\ d_x/l_x$) and $\hat{e}_x$—the mean length of life remaining to each individual alive at the begininng of the year—the life expectation.

Deevey (*op. cit.*) points out that sources of ecological data for the construction of life tables are of three kinds: (1) knowledge of age at death for a random and adequate sample of the population; (2) knowledge of the fate of individuals of a single cohort at frequent intervals; and (3) knowledge of the age-structure among the living. He goes on to remark that information of the first and third types can be used only if one is prepared to assume that the population is stable in time.

For the black-tailed deer we have accumulated data of all three sorts. The deer populations in the chaparral and shrubland we have considered, for the purposes of this analysis, as relatively stable. Those in the wildlife burn are not stable. Life tables, then, may be constructed for the deer populations of the chaparral and the shrubland.

It is of interest to compare the elements of population dynamics displayed by these populations with those of other wild ungulates. Adequate information in which to base sex-separate life tables is available for relatively stable populations of the roe-deer (*Capreolus capreolus*) from Andersen (1953), the red-deer (*Cervus elaphus*) from Evans (1891), and the Dall sheep (*Ovis dalli*) from Murie (1944), providing that certain reasonable assumptions (stated in each case) are allowed.

The black-tailed deer

In constructing life tables from the data previously presented, it has been necessary to extend Table IV (the carcass-tally) so as to break down the 37 months-and-older category into annual age-groups from three to ten. The number of individuals in each age-group was small, but the general pattern seemed to be one of fairly constant mortality rates from three to nine years for does and four to eight years for bucks. This has been tentatively assumed. In extreme old age (arbitrarily considered by us to be about 9-10 years) there is an accelerated mortality, as the oldest deer all die. When techniques of aging become more accurate it may be found that senescence is reached at 12-15 years rather than 9-10, and that mortality is roughly constant all through adulthood. In other words, our assumption that no deer live beyond 10 years may create an artificially abrupt drop-off at the end of the survivorship curve.

It may be seen (in Tables IX and X) that in both range types there is a higher proportional mortality in male fawns; this has been attributed to the higher metabolic rate and nutrient requirements among males (Taber and Dasmann 1954). There is a markedly unbalanced sex ratio by the time two years is reached. At this point the males become vulnerable to predation (hunting) and the females (individuals of which breed for the first time at either 17 or 29 months) to the strains of reproduction. The weight of hunting falls most heavily on the two-year-old class of males, while the loss of females is roughly constant from two to nine years. Both sexes have a higher mortality in the shrubland than in the chaparral. In the adult males this is known to be due to the easier hunting conditions of the shrubland; the deer are easier to kill. In the adult females the higher mortality found in the shrubland is probably related

TABLE IX. Life tables for the black-tailed deer of the chaparral

A. Males

x (years)	l_x	d_x	q_x	$\mathring{e}_x$
0 - 1	1000	526	526	2.3
1 - 2	474	97	204	3.3
2 - 3	377	137	363	3.0
3 - 4	240	75	313	3.4
4 - 5	165	20	121	3.7
5 - 6	145	14	97	3.2
6 - 7	131	14	107	2.5
7 - 8	117	30	256	1.7
8 - 9	87	35	402	1.1
9 - 10	52	52	1000	0.5

B. Females

0 - 1	1000	372	372	4.2
1 - 2	628	41	65	5.3
2 - 3	587	66	112	4.6
3 - 4	521	68	131	4.2
4 - 5	453	67	148	3.7
5 - 6	386	54	140	3.1
6 - 7	332	54	163	2.6
7 - 8	278	54	194	2.0
8 - 9	224	33	147	1.4
9 - 10	191	191	1000	0.5

TABLE X. Life tables for the black-tailed deer of the shrubland

A. Males

x (years)	l_x	d_x	q_x	$\mathring{e}_x$
0 - 1	1000	728	728	1.3
1 - 2	272	36	132	2.5
2 - 3	236	147	623	1.8
3 - 4	89	31	348	2.9
4 - 5	58	12	207	3.2
5 - 6	46	9	196	2.9
6 - 7	37	7	189	2.5
7 - 8	30	6	200	1.9
8 - 9	24	6	250	1.3
9 - 10	18	18	1000	0.5

B. Females

0 - 1	1000	526	526	2.4
1 - 2	474	83	175	3.6
2 - 3	391	82	210	3.2
3 - 4	309	77	249	3.0
4 - 5	232	58	250	2.8
5 - 6	174	44	253	2.5
6 - 7	130	32	246	2.2
7 - 8	98	25	255	1.8
8 - 9	73	18	247	1.3
9 - 10	55	55	1000	0.5

to the higher reproductive rate there. The loss in yearlings from the shrubland range is due, in part, to emigration rather than mortality. This makes an interesting parallel to the situation in roe-deer, described below.

The roe-deer

In 1950 a relatively stable roe-deer population inhabiting some woods on the Danish Game Research Farm at Kalø was exterminated by shooting. Forty-six males, 76 females and 91 fawns were taken. Andersen (1953) has reported on the age-distribution and given data on the occurrence of corpora lutea of pregancy in the females.

Assuming that the annual reproductive rate was relatively constant; that fawns born amounted to 90 per cent of the corpora lutea of pregancy and that the sex ratio at birth was 100 ♂ ♂ : 100 ♀ ♀, we may construct life tables (Table XI) for the two sexes.

It will be noted that there is a high loss not only in the first year of life, but also in the second and especially in the third, in both sexes. Andersen (1953 and personal communication) points out that the hunting kill at Kalø has averaged only 4 ♂ ♂, 4 ♀ ♀ and 6 fawns per year, from 1943 to 1949. He accounts for the loss in young adults in terms of dispersal, citing as evidence the fact that each year roe-deer appear in small outlying woods which are normally uninhabited by roe-deer, and that as many as possible of these are killed. Thus the principal factor limiting this population is apparently not food, as it is in both examples of the black-tailed deer, but emigration. The woods of Kalø seem to have a saturation point for roe-deer, presumably based on intraspecific stress. Darling (1937) has commented on the intolerance of roe-deer for their young of previous years, which he attributes to the patriarchal nature of their social organization.

TABLE XI. Life tables for the roe-deer of Kalø (after Andersen)

A. Males

x (years)	l_x	d_x	q_x	$\mathring{e}_x$
0 - 1	1000	740	740	1.2
1 - 2	260	60	230	2.2
2 - 3	200	110	550	1.7
3 - 4	90	20	222	2.1
4 - 5	70	20	286	1.5
5 - 6	50	30	600	0.9
6 - 7	20	20	1000	0.5

B. Females

0 - 1	1000	630	630	2.6
1 - 2	370	50	135	4.2
2 - 3	320	150	469	3.0
3 - 4	170	50	294	3.3
4 - 5	120	40	333	2.7
5 - 6	80	30	375	2.2
6 - 7	50	20	400	1.7
7 - 8	30	10	333	1.2
8 - 9	20	20	1000	0.5

The red deer

From 1879 onward Henry Evans leased the red-deer shooting on the island of Jura, in Scotland. He conducted an annual census of males (in July) and anterless deer (in February) and classified adult males, yearling (1-2 year) males and adult females and deer under one year of age. He kept a record of deer found dead and, having examined many pregnant females, estimated the production per female. During the first six years he did not burn the heather, and his deer population was roughly stable, the adult females increasing slightly. In the next five years, he was active in heather-burning and his deer population had increased markedly and was still increasing at the time he drew up his report. For present purposes, the information from the first six years only has been used. The basic data are (averages for 1879-1884) inclusive):

Stags (2 years and above) alive in July—460
Shot— 60
Dying from other causes— 31

Hinds (one year old and above)
alive in Feb.—612
Shot— 5
Dying from other causes— 47

Hinds first breed at 2½ years, 100 hinds (one year old and above) bring 37 calves to February and 30 to one year of age. Of these 30, 13 are ♂ ♂—these have little loss to 3 years, and 17 are ♀ ♀—these become 15 by second birthday and are still 15 at third birthday. The sex ratio at birth is 100 ♂ ♂ : 100 ♀ ♀ (Evans 1891).

A maximum life span is assumed as 15 years (by the present authors).

The life tables have been derived from these data (Table XII).

TABLE XII. Life tables for the red deer of Jura (after Evans)

A. Males

x (years)	l_x	d_x	q_x	$\mathring{e}_x$
0 - 1	1000	610	610	2.9
1 - 2	390	...	...	5.6
2 - 3	390	5	128	4.6
3 - 4	385	26	675	3.6
4 - 5	359	65	181	2.9
5 - 6	294	86	293	2.4
6 - 7	208	61	293	2.2
7 - 8	147	60	408	1.7
8 - 9	87	35	402	1.8
9 - 10	52	22	423	1.7
10 - 11	30	13	433	1.5
11 - 12	17	8	471	1.3
12 - 13	9	5	556	0.9
13 - 14	4	4	1000	0.5

B. Females

0 - 1	1000	485	485	3.1
1 - 2	515	60	117	4.5
2 - 3	455	...	...	4.0
3 - 4	455	126	277	3.0
4 - 5	329	91	276	3.0
5 - 6	238	65	273	3.0
6 - 7	173	48	278	2.9
7 - 8	125	35	280	2.8
8 - 9	90	25	278	2.7
9 - 10	65	18	277	2.6
10 - 11	47	13	277	2.4
11 - 12	34	10	294	2.1
12 - 13	24	7	293	1.7
13 - 14	17	5	294	1.2
14 - 15	12	12	1000	0.5

As in the black-tailed deer described above, these red deer died principally of starvation and exposure, except for a light harvest of adult stags. An effort was made by Evans to kill only mature stags, so there is not the heavy mortality of young adult males noted for the black-tailed deer.

The Dall sheep

From 1939 to 1941 Adolph Murie, working in Dall sheep habitat near Mt. McKinley, where wolves were common, recorded the age, sex and probable year of death of every sheep carcass he could find (Murie 1944). Taking only those which died from 1937 to 1941, when the population was relatively stable, it is possible to construct life tables (Table XIII) for the two sexes if the following surmises are accepted:

TABLE XIII. Life tables for the Dall sheep of Mt. McKinley (after Murie)

A. Males

x (years)	l_x	d_x	q_x	$\mathring{e}_x$
0 - 1	1000	718	718	3.3
1 - 2	282	20	71	9.3
2 - 3	262	3	11	9.0
3 - 4	259	...	...	8.1
4 - 5	259	3	11	7.0
5- 6	256	5	20	6.1
6 - 7	251	...	...	5.2
7 - 8	251	14	56	4.2
8 - 9	237	6	25	3.5
9 - 10	231	28	120	2.5
10 - 11	203	40	200	1.8
11 - 12	163	70	429	1.1
12 - 13	93	87	935	0.6
13 - 14	6	...	...	1.5
14 - 15	6	6	1000	0.5

B. Females

0 - 1	1000	718	718	2.8
1 - 2	282	28	99	7.6
2 - 3	254	6	24	7.4
3 - 4	248	3	12	6.6
4 - 5	245	3	12	5.6
5 - 6	242	8	33	4.7
6 - 7	234	17	73	3.8
7 - 8	217	9	41	3.1
8 - 9	208	11	53	2.2
9 - 10	197	93	472	1.3
10 - 11	104	59	567	1.0
11 - 12	45	36	800	0.7
12 - 13	9	9	1000	0.5

Ewes first breed at 2.5 years.

Average production per adult ewe is 1.0 lamb.

The sex ratio at birth is 100 ♂ ♂ : 100 ♀ ♀.

The loss of yearlings is not more than 10 per cent.

The sheep which could not be aged exactly because the horns were missing, but which were known to be at least nine years old, had the same age-distribution as the 9-year-plus-older sheep which could be aged from the horns.

These data show for both sexes a low rate of loss between the first and ninth year. The animals were not subjected to hunting, but they were constantly under rather heavy pressure from wolves, which took mainly the lambs and very old adults. This apparently left the prime animals, according to Murie's range observations, with ample food supplies and a high life expectancy.

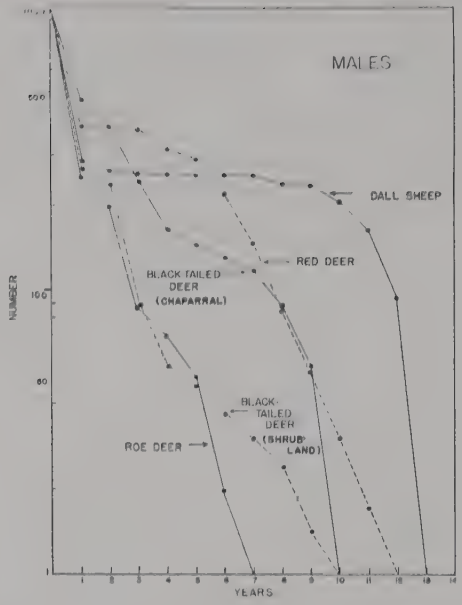

FIG. 1. Survivorship curves for males of five ungulate populations.

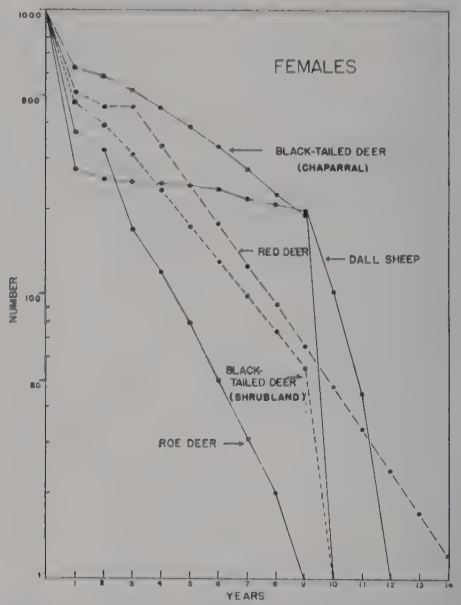

FIG. 2. Survivorship curves for females of five ungulate populations.

Population characteristics

When survivorship curves, based on the l_x columns in the life tables, are plotted, as in Figures 1 and 2, various segments may be compared. Both sexes of all the species are alike in having a very steep initial slope, indicating a high mortality during the first year of life.

Among the males the loss during the second year of life is small in all species except the roe-deer, where there is emigration, and the black-tailed deer of the chaparral where some yearlings are lost, partly through being mistaken for older deer by hunters. During the third year of life there is a heavy loss among roe-deer and black-tailed deer from both range types. The roe-deer loss is due to emigration. That in the black-tailed deer is due to hunting. In the Dall sheep and the red deer there is little loss during the third year. From the fourth year onward to old age the hunted populations (roe-deer, black-tailed deer and red deer) show fairly steep losses. The rate of loss tends to become less in full adulthood in the black-tailed deer, because learning and behavior make these individuals less vulnerable to hunting. In the red deer the rate of loss becomes heavier in full adulthood because of the selection of prime stags by the hunter. The Dall sheep, which is not hunted, shows very little loss from adulthood to old age. If it were not for hunting, the other male populations would exhibit survivorship curves more nearly like that of the Dall sheep, but it is doubtful if they could ever attain as high a survivorship as long as their ranges were fully stocked and starvation was a common cause of death. The effects of competition are discussed below. The stress imposed by the annual growth and shedding of antlers, peculiar to the Cervidae, is another factor, of unknown magnitude.

In old age there tends to be a steepening of the survivorship curve—the accelerated loss due to senescence—especially in the Dall sheep. The red deer do not display this, because the high kill by hunting permits few individuals to grow old.

Among the females there is a small loss during the second year of life in all examples. In none of these populations do the females regularly bear young at one year of age. In the roe-deer and the black-tailed deer the usual time of first bearing is on the second birthday, although some black-tailed deer, especially from the chaparral, do not bear until three years old. The red deer and Dall sheep bear first at three years.

After the third year of life all examples have a rate of loss similar to that maintained until old age. In general, there is an inverse relationship between production of young and survival of breeding females. Presumably this is due to the fact that on any fully-stocked herbivore range there tends to be

competition for forage, and the more successful is the reproduction, the keener is the competition. The survival of adult females may be lowered still further if they are hunted, as was true to a limited extent for the red deer of Jura. On the other hand, the survival of adult females may be raised if there is a removal of the competing members of the population. This was the situation for the Dall sheep of Mt. McKinley, where both the very young and very old were removed by wolves. The roe-deer population was also periodically lowered, reducing competition; the reduction there was caused by emigration. However, there was also a hunting loss among the adult females, and this tended to cancel the advantage conferred upon them by the emigration of the young.

The most clear-cut example among the present cases is the comparison of survival between the adult deer of the chaparral and those of shrubland. In December, when weaning is long past and the young of the year are in direct competition with the old for food, the chaparral population contains 0.53 fawn for every adult doe. The shrubland population contains 0.76 fawn for every adult doe (Tables VI and VIII). The values for life expectation of prime (3- to 6-year-old) does ranged in chaparral from 4.2 to 2.6 years and in shrubland from 3.0 to 2.2 years. Fawn production to December in chaparral is about 70 per cent of that of shrubland; life expectation in shrubland is about 78 per cent of that in chaparral. The comparison could be expanded to include the whole population of both sexes—taking the fawns plus yearlings on the one hand as the production, and all older deer together as the producers. The result would be much the same; the greater the proportional production, the shorter the life expectancy of the producers.

It seems that most of the differences between these various populations are not inherent in the species, but rather are imposed by environmental conditions. The limitation of the roe-deer population by emigration, for example, would be effective only if the population occupied an island of habitat, surrounded by uninhabited areas into which the emigrants could disappear and from which none would come to replace them. The situation in the shrubland is similar, but the island-like nature of the habitat is less marked, and an immigration from the surrounding low-density population may partially balance emigration. In the chaparral, which is merely an artificially designated area in a large region of similar habitat, emigration and immigration should balance.

If a roe-deer population is fenced, Andersen points out (*in litt.*) that winter mortality due to starvation is high. In such a case it would be expected that the population dynamics would be different from those found at Kalø, since the older deer would be competing with younger, physiologically more efficient animals.

Similarly, if a Dall sheep herd were not culled by predators, the population would presumably be limited by food supplies, and the mortality among prime adults would increase accordingly.

These considerations point up the danger of considering the population dynamics of a given animal under given circumstances as typical of that species in general.

Summary

Population dynamics have been reconstructed for three natural populations of the Columbian black-tailed deer (*Odocoileus hemionus columbianus* (Richardson)) which differed from each other in habitat. The three habitats, chaparral, shrubland and wildfire burn, were all modifications by man of the chaparral association of the North Coast Range of California. Chaparral is a densely-growing association of shrubs; shrubland is a shrub-herb interspersion; wildfire burn is chaparral recently burned, where the shrubs are sprouting from the root-crown. These populations were compared for stability, density, structure, reproduction, mortality and movement. The principal causes of mortality were hunting (adult bucks) and starvation (other classes). The details of population gain and loss through one typical year (four years for wildfire burn) were reconstructed from these data. Some characteristics of the three populations were:

Table XIV

	Chaparral	Shrubland	Wildfire burn (First year following burning)
Population density (Deer per square mile)			
July	33	84	112
December	27	64	86
Reproduction (fawns per 100 adult ♀♀)	0.77	1.05	1.32
Importance of movement in population gain or loss	none	little (yearling does)	great (all classes)

Populations in chaparral and shrubland were relatively stable, so life tables were prepared for them, the sexes being treated separately. The population on the wildfire burn was unstable, high at first due to influx and then dropping rapidly due to egress, increased mortality and decreased reproduction.

Sex-specific life tables for the deer of chaparral and shrubland were compared with those for: a hunted red-deer population on a fully-stocked island; a hunted roe-deer population from which there was heavy emigration; and an unhunted Dall sheep population under heavy predation by wolves.

Some characteristics of these populations were:

TABLE XV

	Average annual population loss (per cent)		Loss during first year of life (per cent)		Life expectancy from birth (years)	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Black-tailed deer						
Chaparral	36	22	53	37	2.3	4.2
Shrubland	55	34	73	53	1.3	2.4
Red deer	30	28	61	49	2.9	3.1
Roe deer	59	46	74	63	1.2	2.6
Dall sheep	42	30	72	72	3.3	2.8

On fully-stocked ranges there is an inverse relationship between production of young and survival of breeding adults, due presumably to competion for food between young and adults. When young (or senescent) are removed, by predation or emigration, the chances for survival of breeding adults appear to be improved.

The differences in dynamics between these various populations of different species, are apparently due more to environment than to heredity.

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THE ECOLOGY OF THE PILEATED WOODPECKER

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PREFACE

The following material is based largely upon the findings of my husband, the late J. Southgate Y. Hoyt, in connection with his studies for his doctorate, which he received in 1948, together with some additional material of my own. For the sake of clarity and ease of reading, I have decided to make no attempt to indicate the information quoted directly from his thesis, by use of quotation marks or page references. Nevertheless the credit for the work should go in his memory and not to this writer, who acts chiefly as compiler. However, I assisted in much of the work done in 1941 and thereafter.

I am indebted to Arthur A. Allen for critcial reading of the manuscript.

GENERAL BASIS OF STUDY

The pileated woodpecker (*Dryocopus pileatus*), has a range which covers most of wooded North America. In most areas of its range, the pileated woodpecker had decreased alarmingly by

the turn of the last century. In fact throughout the first quarter of the 20th century it was exceedingly scarce in places where it had once been abundant and many feared that it was doomed as the ivory-bill seemed to be. But then the numbers began to increase slowly, for reasons which are still not entirely clear, and the species began to lose some of its former shyness in many places. The life history material to be presented now is based upon work which was done mostly in the years '38-'42, when the pileated was somewhat rarer than now (1956) and certain aspects of its behavior will probably be modified with increased competition for food and desirable territories.

Most of our observations were made on a pair which roosted and nested in a 120 acre woodlot known as Sapsucker Woods, about three miles northeast of the Cornell University campus. Additional study was made of a pair in the Six-Mile Creek watershed on the southeastern edge of Ithaca, and in the spring of 1939 the nest of this latter pair was chosen for particular study, as it was more accessible that year than the one in Sapsucker Woods. The general feeding area of other pairs within a 15 mile radius of Ithaca was noted, and observations were made on these birds as time would permit.

Throughout the winter, during the years '38-'42, visits were made to Sapsucker Woods three or four times a week, and the birds watched for several hours each time. When spring came, observations were made daily and often twice daily, throughout the period of courtship and nesting. Since 1945, additional observations have been made at Sapsucker Woods at less frequent intervals.

Abundance

Around 1945 there were, within a radius of 15 miles of Ithaca, N. Y., at least 12 pairs of pileateds.[1] In 1955 I estimated 15-18 pairs in the same area. All reports I have received indicate that the population is higher than this in the areas of virgin timber in the south. In extensive areas of swampland in southern United States, it is understandable that ranges of pairs may overlap. In the Ithaca, N. Y. area, woodlots are not large. A pair tends to be restricted to a given woodlot, and while that pair may range somewhat beyond the borders of the woodlot, very rarely is more than one pair found in a single woods. This fact will serve to influence the behavior of the birds, with somewhat less competition for food and nesting sites than in the south.

Not only are the birds becoming more numerous in the localities where they were previously found, but they are taking up new abodes, thus spreading their local range over new territories. Undoubtedly this represents the spreading out of the young birds. Because of the scarcity of banding records of this species, little is known about the wanderings of young birds from the nesting site, but one case (S. Hoyt 1952), indicated that a young bird had moved to a spot approximately 20 miles from the place where it was hatched.

Food and Feeding Habits

In the fall of the year the pileated woodpecker may be found feeding on many species of fruits as well as mast in the form of wild nuts. Herbert Stoddard, for example, has had a pair feed for many years on pecans at his plantation near Thomasville, Georgia, and recently he has attracted them to artificial food consisting of suet mixed with ground pecan meats. This is one of the few cases of pileateds coming to feeders, and will be discussed more fully in another paper.

Of the vegetable foods listed by Beal (1895, p. 32) the commonest in the north-east, according to my observations are wild grape (*Vitis cordifolia*), Virginia creeper (*Parthenocissus quinquefolia*), sumac (*Rhus copallina*) and wild cherry (*Prunus pennsylvanica*). I have also had reports of pileateds feeding on poison ivy (*Rhus toxicodendron*) and several of the dogwoods (*Cornus* sp.) in the Ithaca area.

In the winter, the diet of the pileated woodpecker consists chiefly of insects, particularly carpenter ants (*Campanotus herculeanus*) which live in colonies deep in the heart of forest trees. In woodlots near Ithaca, many pines and beeches are attacked by these insects, and continue to look perfectly healthy externally, even after the heart has been eaten out. Power poles and abandoned dwellings or other man-made structures may also be riddled by the tunnels of these ants, which are frequently located and cleaned out by the pileateds. The larvae of various species of wood-boring beetles are also taken by the bird, and since many of these are found close beneath the bark, older trees so infested may show patches of bark stripped off. Theories as to how the woodpeckers locate ant colonies have been considered in another paper (J. S. Y. Hoyt 1950a) and will not be repeated here. These woodpeckers have come under serious attack in recent years for their destruction of power poles in some areas. Many ornithologists are still convinced that such poles have been attacked first by insects, as the damaged poles are usually those in remote areas where much of the dead and standing timber has been cleared out for the power lines. The carpenter

ants and other insects naturally move into the poles when erected. At present writing, however, evidence in this matter is inconclusive.

In the spring the diet of the woodpeckers seems to consist of a large percentage of larvae of wood-boring beetles, and at this time of the year the birds may be surprised working near the ground on stumps or rotten logs. A greater variety of insect life is taken during the summer, quite naturally, including flies, moths, mosquitoes and the favorite ants and grubs. For the entire year, animal matter seems to make up about 75% of the diet, vegetable 25%.

Voice

It was noted that the call of the female is higher in pitch than that of the male, but it has not always been possible to name the sex if only one bird called at a time. In winter the birds are relatively silent, but in spring may be heard calling at any time throughout the day.

Roosting

The hole used for roosting may resemble a nest hole, but seems to be located usually in a live tree whereas a nest hole is not necessarily so. Roost holes are frequently very high in a tree, even sixty or seventy feet, but may also be fairly low. One hole that was often used by the male pileated under observation for a number of years was just twelve feet from the ground. The depth of the holes seems to vary as does the size of the entrance. One hole measured was nineteen inches deep and another measured twenty-three inches. Bent (1939, p. 181) quotes Maurice Brooks as stating that "Nesting cavities are sometimes used as roosting places after the nesting season," but it was my experience that the nests of the pileateds in one woodlot for ten years were not used by this species again for any purpose, although they were utilized by wood ducks, flying squirrels, starlings, etc. Nor, contrary to Brooks' observation, have I ever seen more than one bird enter a roost hole. In my experience, likewise, the same few roost holes were used for several years, the male bird having several between which he alternated, and the female several others.

Early in the study the night roosts were located of both birds in the pair under particular study and almost daily observations were made throughout six winters to determine the time of going into the roost and the time of leaving. It was found that the male bird used the same roost most nights during six winters between 1938 and 1947, but observations were not made during the war years of 1942-1945, when the observers were in service. During the nesting period, as will be brought out later, the male stayed on the nest, and his roost was not occupied. Also throughout the summer, for a period of about two months after the young had left the nest, the male was not found at his winter roost, but from the end of August until the next nesting season, the known roost was occupied. When the observer was not well concealed, the male usually flew to his customary roost, bobbed about on the tree, gave a few sharp pecks and an occasional call, and then flew off to another section of the woods, evidently to occupy one of his other roost holes. The female of this pair varied her roost hole for no apparent reason. The one she used most often was within fifty feet of the male's.

An attempt was made to ascertain what factors were involved in the time of going to roost and time of arising; upon each visit to the area, the time was noted, as well as temperature, weather conditions, amount of light as read on a Weston exposure meter, and the time of sunset and sunrise. One factor that could not be measured and which might have had some significance, was the light conditions in the woodlot where the bird was feeding before coming to the roost, but probably the difference was slight. The data obtained were carefully plotted on a graph, but no significant correlation seemed to exist. However, certain tendencies were noted and some generalizations can be made. The female usually entered the woods and her roost hole a few minutes before the male. Both birds went to roost about a half-hour before sunset, with the actual time varying somewhat with weather conditions. Temperature seemed to have no effect, but in very adverse weather the birds entered the roost hole much earlier and left later in the morning.

A single male pileated that was under observation for a short time in Memphis, Tennessee in 1944-45 behaved in a similar manner.

Both pileated woodpeckers left the roosting hole before sunrise in the morning and usually called either from the hole or from a spot nearby. Both were relatively late risers among the woodpeckers, for downies, hairies and flickers were usually heard or seen for from 15 to 30 minutes before the pileateds emerged from their roost holes, during the winter and early spring.

Nesting

Habitat Requirement

The nest of the pileated woodpecker is usually placed in the same woods in which the birds spend most of the time. Forbush (1927, p. 281) de-

scribes the nesting habitat as being "in a forest of heavy timber, often of second growth and consisting of mixed deciduous and conifers." While nests may be located on the side of a mountain, more of them are found in lowlands such as valleys or bottomland. One of the requirements may possibly be water, for few if any nests in the writer's experience have been located far from a supply of water of some kind. Some nests have been found in trees standing in water in swampy areas, others near a stream or lake. However, what the connection could be is not clear, and it may be coincidence.

The importance of territory in the northern woods of the pileated woodpecker range is difficult to determine since there are so few birds that competition does not often take place. In the south where many birds nest in more limited areas, there may well be fights over territorial boundaries, but I have no records to indicate this nor have I been able to find anyone who has witnessed such a thing. How territory is selected, or which bird selects the nesting site, has not yet been determined.

To what extent the pileated will defend its territory against any other species of woodpecker is also open to question. Dr. James Tanner reported, in conversation, seeing a pileated and a flicker fighting over a nest hole for several minutes, with the pileated driving away the flicker. The writer observed in 1947 a pileated, upon leaving the nest during incubation, dive at and drive away a flicker which had landed on a stub not far from the nest hole. On the other hand, in 1939, near Ithaca, a pileated and a flicker nested on opposite sides in the same stub at the same time, and paid no attention to one another (J. S. Y. Hoyt 1948).

With any smaller hole-nesting birds, the pileated probably has little difficulty. Baird, Brewer and Ridgway (1905, p. 551-552) give an observation by the Rev. Dr. Bachman as follows: ". . . a pair of Pileated Woodpeckers building a nest in an old elm-tree in a swamp, occupied it the first year. Early the next spring two Bluebirds took possession of it, and there had young. Before they were half grown, the woodpeckers returned to the place, and, despite the cries and reiterated attacks of the Bluebirds, took out the young and carried them away to some distance. Next, the nest itself was disposed of, the hole cleaned and enlarged and there they raised their brood."

An instance of parasitism by a starling was observed by the writer in 1941 and has been reported in detail elsewhere (J. S. Y. Hoyt 1948). The pileated hatched the starling egg, but the young starling soon died and was carried out of the nest by the second day after hatching. Starlings apparently have little chance of success in taking over a hole in which a pileated pair is interested, but in 1942 near Ithaca starlings nested successfully in a hole in the same tree with the pileateds. Apparently the parasitism in '41 resulted because the woodpeckers were able to drive away the starling after one egg had been laid.

Courtship

The song (if such it may be called) of the pileated woodpecker is very difficult to express in words. Forbush (1927, p. 281) describes the love note as follows: "a-wuck, a-wuck," after a description by H. Nehrling. When I have heard the "love notes" given during a courtship performance, they sounded like a descending nasal "kyow-kyow-kyow-kyow," often repeated as many as six times, usually not more than ten times. The birds vary this call a little by the volume with which it is produced. When the call is given in a relatively soft tone, it has much less of the nasal quality. Bent (1939, p. 187) quotes Dr. George Sutton as describing another call given during the nesting season, as "whining notes, suggesting the *mew* of the Yellow-bellied Sapsucker." Bent goes on to say that this call to which Dr. Sutton refers is more than that and is like a loud cry, resembling the scream of a hawk. This, he says, is uttered slowly five or six times. A number of times when the Ithaca pair was together prior to nesting and frequently during nesting, a soft, nasal "chuck-chuck-chuck" call was heard, entirely different from other calls already mentioned. Once this call, or a slight variation of it, was given during nest-changing.

Both sexes participate in the vocal part of their courtship performances. One or the other starts the call, which is soon picked up by the other. The birds have been heard to duet, sounding as one bird but with one call lower than the other. These notes may be given in unison, or in such rapid succession that it sounds like one bird calling in double time.

Besides calling, the birds also resort, as do other woodpeckers, to drumming. This drumming is produced by the bird on a solid dead limb, which seems to act as a sounding board. A good description of the drumming procedure was given by Vickers in 1914 (p. 15), and the latter believed that this drum in proper atmospheric conditions might be heard a distance of two miles. The bird may relax between drums to the extent of hopping about on the limb, cocking his head, or preening.

There seems to be no constant number of times

that the birds drum, even if undisturbed. Male and female both participate, with no apparent difference in type or volume of drum. On one occasion, what might have been the selection of a place was observed. The male bird alighted on the dead limb at the top of a tree, began to climb it, and pecked hard at one place after another. Finally he struck a spot which gave a deep hollow sound, and there he remained, to drum repeatedly. Having once established a drumming place, the birds often return to the same place time after time and in some instances year after year. Several drumming localities may be found within one nesting area. The birds sometimes move from one limb to another on an almost regular circuit. Prior to the nesting season, most of the drumming is done in the morning and evening, when the two birds are together on the roosting ground.

Sutton, in Bent (1939, p. 175) told of listening to a male drumming for over an hour. "At least fifty or sixty times there was an introductory, rapidly given roll; then a pause, followed by three distinct blows." Such following blows have been heard by others occasionally, but not with any such regularity.

Display

While I have been unable to find any recorded description of the act of mating in the pileated woodpecker, there have been a number of observations of courtship display, which resembles to some extent that of flickers. Bent (1939) and Forbush (1927) have given good accounts of the "courtship dance" as described by several witnesses. This dance has been seen both in spring and fall, and involves bowing and nodding, crest elevation and depression, wing-spreading and bill touching. Soft calls are sometimes given, according to these witnesses.

David G. Allen (personal communication) has reported seeing the courtship dance taking place on the ground. In March of 1956 he watched a pair for ten or fifteen minutes, bobbing, rocking and hopping about in the snow in Sapsucker Woods Sanctuary near Ithaca. At times one bird or both would climb a short distance up a nearby oak, dance around the trunk and back again, then drop to the ground. At times the bills of both birds would be pointed straight up as they rocked back and forth, then they would seem to jab at the ground. He could hear no sounds while this was going on.

According to my own observations, based on pairs around Ithaca, the male bird usually flies in circles through the tree tops, calling a soft "cuk-cuk-cuk," at times flashing the white of his wings more than in normal flight. Throughout this performance the female is frequently in a more or less exposed position on a limb, rocking her body from side to side. After several minutes of this performance, the male drops to the tree where the female is perched, at which time she gives a loud nasal mewing call audible for a hundred feet or more. The male works his way up the tree onto the limb where the female is sitting. Often the male will answer the female's mewing with a similar call, taking sometimes as long as ten minutes to get to the limb with the female. When within about twenty feet of her the male spreads first one wing, then the other above his back, exhibiting the beautiful black and white pattern. At this time the crests of both birds are erect and brilliant scarlet. At this point in my recorded observations, first the female and then the male has flown off to a distant spot, perhaps to repeat the performance. They may alight momentarily on the tree trunk, but have always passed from my sight. I have never witnessed this courtship performance outside the woods in which the nest is or will be located and where the birds always roost—*i.e.*, never in a woodlot used only for feeding.

From what I have seen of the courtship performance, it is my belief that mating takes place while the pair is on a horizontal limb, probably sitting lengthwise. However, A. A. Allen (personal communication) reports seeing hairy woodpeckers mate while sitting crosswise. The described courtship activities were observed either in the morning about an hour after they had left the roost or in the evening, within a two hour period before roosting. In central New York State this portion of their courtship begins in early April and lasts through the month, but one observation was made of a less pronounced performance in the last week of March.

The Nest

The nest is usually placed within the boundary of the winter range and not far from the winter roosts. The same nest tree may be used several years, but new holes are usually dug for each year's brood. Either a dead tree, or dead limbs of live trees seem to be preferred, although there are a very few cases of a nest being located in live wood. Various observers have noted that the birds may make several 'false starts,' beginning a hole, and then abandoning it for some reason. In one case under observation, it appeared that a nest hole was almost if not entirely completed, then abandoned and a new nest dug in the same dead stub, on the other side and a few feet higher. Nests have been found (Bent, p. 176 and this writer)

in beech, poplar, tulip poplar, birches, oak, hickories, several species of maple, hemlock, pine, ash, elm and basswood. In the woodlot under particular study near Ithaca, most nests have been in beeches. Height from the ground has been found to vary from 15 to 70 feet (Bent). The nest involved in the writer's study in 1939 was 28 ft. from the ground, the one studied in 1941 was 35 feet up. There seems to be no preference as to direction the hole faces. Nests have been watched near Ithaca which faced in all directions.

Both birds participate in digging the hole, but as with other species of woodpeckers, the male does the greater part of the work.

In a study of a nest in 1939, the following measurements were noted: the entrance hole 3-¼ by 4-¼ inches in diameter; from the surface of the bark to the back of the nest 10-¾ inches; the cavity itself 8-¼ inches in diameter and 15 inches deep. The tree was 17-½ inches in diameter at the nest entrance. Measurements of the nest studied in 1941 are comparable, except that the hole was deeper in the tree, and both sets of measurements compare well with those recorded by Bent (1939). According to Bent depths may vary from 10 to 24 inches, with extremes of 6 to 26 on record (p. 177). (Forbush says 12-30 inches, p. 281.). It is difficult to understand how a pileated could mange with a nest hole only 6 inches deep!

In most cases the bottom of the nest is practically bare with only a few chips of wood taken from the sides in digging. Here the eggs are laid. Forbush (1927, p. 281) stated that on rare occasions a little sand may be found on the floor of the nest. In the 1939 nest under our observation, six very small pebbles, with a very small amount of fine sand, were present. This might, of course, have been regurgitated material.

Nests are most easily located by looking for the quantity of large chips scattered all over the ground beneath the nest tree, and even 15-20 feet from the tree. The old holes may be taken over by other birds, including wood ducks, and other animals, especially flying squirrels.

The Eggs

Bent (1939, p. 179) describes the egg of the pileated as being "white with a gleaming smoothness and translucence of shell." I would add that the texture of the shell is that of a very fine-grade, thin white china. As incubation progresses, the egg takes on a darker and more cloudy color. The pileated egg seems small for the size of the bird. Bent (1939, p. 179) gives the average of 51 eggs as being 33.16 by 25.21 millimeters. I have found no published data on weights, but the 8 eggs in the two nests under particular study weighed as follows: in the '39 nest, 11.4, 10.7, 11.3, and 9.8 grams. The last egg did not hatch. In the '41 nest the eggs weighed 10.4, 12.4, 12.2, and 10.5 grams 12 days before hatching. I failed to note which of these was the infertile one, but twelve days later when three eggs had hatched, my notes indicate that the unhatched egg weighed 10.0. The eggs are rather broadly oval, both ends being flatly rounded. The usual complement is four, but sometimes only three are laid. Reports of five eggs have been published by Wheeler (1921, p. 152) and Stockard (1940, p. 465). The literature contains a few undocumented reports of six eggs (for example, Bendire, 1895, p. 107) and even one of eight (*Ibid.*).

If the eggs are removed the birds usually lay again, sometimes in the same nest. This is not always the case, and Stockard (1904) reports removing eggs from four nests without the birds re-nesting. Carriger and Wells (1919, p. 153) record a third set, after two sets were removed. In any case, more than one brood has never been recorded in one season for this species.

Incubation

Bendire (1895, p. 107) gave the incubation period of the pileated as "about 18 days," and Burns (1915, p. 284) also said 18 days. We found this to be correct (J. S. Y. Hoyt 1941, p. 528). In 1939 incubation commenced on April 29 and on May 16 there were young in the nest. In 1941, the 4th egg was laid on April 22 and newly hatched young were found in the nest on May 10th.

As is the case with several other species of woodpeckers (see Allen and Kellogg 1937, p. 171, on ivory-bill) the male is as attentive as the female during incubation, and in those cases in which times were carefully noted, the male spent more time incubating than the female. The male spends the night on the nest, and somewhat more time during the day. The bird not on the nest will remain in the woods nearby, feeding, flying from place to place and often calling. The male often visits one of his favorite drumming spots. Periods on the nest seemed to average about two hours. The change of birds at the nest is usually conducted with a certain amount of ceremony. The bird which is off the nest frequently calls from a nearby tree before actually coming to the nest. When this call is heard, the bird within the nest comes to the entrance, sticks its head out and looks around, often giving a soft nasal "chuck." In every case we observed, except one, the bird on the nest remained there until the mate had

come to the nest tree. In the exceptional case the female flew from the nest and joined the male when both gave a few soft "chucks," before the male went to the nest.

Often, when the 'off' bird has landed on the nest tree, the bird within the hole will rap several times on the inside, then will leave as the other bird approaches the entrance. As Bent noted (1939, p. 180) the birds tend to have a regular path of approach to the nest, and we noted that the bird leaving tended to fly off in the same direction each time. There may be a soft conversational exchange at the nest entrance, and the 'relief' bird usually comes to the entrance for a look around immediately after entering, then disappears into the hole. During the period on the nest, the bird may come to the entrance and remain there for some minutes, looking around. While many have reported the birds to be so timid that they will flush from the nest at the slightest disturbance, the pair we had under observation never did so, often watching us at the foot of the tree. They may, of course, have become accustomed to our presence.

Our notes indicate that during the approximately 14 hours of daylight at this time of year, the female spent six on the nest, the male eight, plus ten during the night. During the 14 hours, the birds changed places from 8 to 10 times, and as night approached the period on the nest was apt to be only an hour instead of two.

The detailed notes of activities during incubation show that the male did some quiet digging and chiseling around the inside of the hole during some of his 'shifts.' For example, at 5:45 P.M. on May 4, 1939 (the sixth day) I noted: "Male chiselled some more wood from the sides and appeared at the entrance once in awhile to drop some soft chips over the sides" which might be interpreted as a restlessness or boredom or is perhaps comparable to the acts of certain ground-nesting birds which frequently reach out for sticks or grass or other nesting materials.

At this time of the year most of the food is obtained from the bark or branches. No deep digging is attempted. The birds may be surprised on fallen logs or low tree stumps, which may have been lying there all winter and perhaps contain a readily available supply of insects now. Using this source of supply fits in with their habit of remaining close to the nest tree, rather than wandering to far points of their usual winter range.

While the birds are noisier in general at this time of year, they are relatively quiet near the nest, and their conversations at the nest, as already noted, seem muffled.

Although many birds carry away the shells after the eggs hatch, the pileated seems to leave the shells in the nest, where they are soon ground up and mixed with the chips on the bottom of the nest. In the 1939 nest under observation, the unhatched egg remained in the nest for a week after the others hatched. On the 9th day it was gone, but whether it was broken or carried away I do not know. In 1941 the infertile egg was removed from the nest by the writer.

The development of the young woodpeckers in the nest has been described in a publication (J. S. Y. Hoyt 1944) and will not be repeated here, except to summarize the findings, based on the 1939 nest. The eyes open first on the eighth day; the ear is developed as a depression in the side of the head and is fully developed by the tenth day. Pin feathers first appear on the third day, and by the tenth day feathers have broken their sheaths and are starting to cover the body; on the twelfth day the young are fed at the entrance to the nest rather than at the bottom of the hole, and the young are ready to leave on the 26th day. The sex of the young birds can be determined on the 8th day, by the color of the developing feathers of the forehead and 'moustache.'

The young of the 1941 nest about six to ten hours after hatching weighed 15.8, 18.0 and 24.5 grams. The lightest bird died on the eighth day and was carried out by one of the parents. On the 25th day, the surviving two weighed 223.2 and 211.2 grams, having reversed their weight relationship.

Measurements were taken each day on one of the young and are presented in Table I: upper mandible from the base, lower mandible from the commissural point, tarsus, hallux, middle toe including nail, second primary feather (from outside), third primary and central rectrix from the base.

Parental Care

The parent birds are very attentive to their young. While incubation is taking place, as already mentioned, the male assumes most of the responsibility, and he seems to continue this while the young are in the nest. Usually when we approached the nest, it was the male we flushed from within. The male likewise always brooded the young overnight, the female seeking a roost near at hand.

Food for the young seemed to consist of ants for the most part, but occasionally caterpillars and other forms of insect life may be fed. On one

TABLE I. Measurements of one young pileated woodpecker from 1941 nest (hatched May 10)

Date	Upper mand. from base	Lower mand. from comm. angle	Tarsus	Hallux	Middle toe
	mm	mm	mm	mm	mm
May 11	11.0	17.0	19.2	6.0	10.2
12	12.5	19.0	21.0	7.2	12.0
13	14.0	20.9	22.8	7.8	15.1
14	15.4	22.8	27.0	9.0	16.0
15	16.9	24.0	29.0	10.0	20.0
16	17.0	24.4	31.0	11.5	22.9
17	18.2	25.8	34.1	13.7	25.2
18	19.5	27.0	35.5	15.0	27.3
19	21.0	29.0	36.5	15.0	30.9
20	21.5	29.0	37.0	16.0	31.0
21	22.5	30.9	38.0	19.0	32.0
22	24.0	32.0	39.5	19.0	33.0
23	26.0	33.4	40.0	19.0	34.0
24	27.0	33.8	41.5	20.2	34.5
25	28.0	34.0	41.5	20.0	35.3
26	29.0	34.5	39.0	20.0	37.5
27	29.8	35.0	40.0	20.5	37.0
28	30.0	35.0	40.2	20.5	37.0
29	31.6	36.4	40.6	21.0	37.0
30	32.6	37.4	41.0	21.0	37.0
31	33.5	38.2	41.0	21.0	37.0
June 1	35.0	38.2	41.0	21.0	37.0
2	35.5	38.3	41.0	21.0	37.0
3	36.0	....	....	....	....

Date	Wing from head of humerus	2nd primary	3rd primary	Central rectrix from base
	mm	mm	mm	mm
May 11	33.0	....	....	....
12	37.0	....	....	....
13	47.8	....	....	....
14	56.3	....	....	....
15	63.0	....	....	....
16	72.0	2.1	....	1.1
17	79.1	4.6	....	2.0
18	86.2	7.1	....	3.2
19	93.2	11.1	13.0	4.1
20	....	17.0	19.0	6.0
21	....	22.5	24.0	10.8
22	....	28.1	30.1	15.2
23	....	33.1	37.0	20.5
24	....	41.5	44.4	26.8
25	....	46.2	50.0	29.3
26	....	52.0	57.5	38.0
27	....	59.0	66.5	42.0
28	....	64.1	70.2	47.1
29	....	71.0	80.0	51.9
30	....	77.0	84.6	54.9
31	....	80.0	91.1	59.9
June 1	....	90.0	97.0	65.0
2	....	97.9	107.5	66.0
....	....	....	....	....
6	....	....	....	89.0

occasion when the young were removed for weighing, a few ants were found sticking to the mouth of one bird. On another occasion, while weighing the birds, one young defecated. The feces were enclosed in a tough but soft membrane, which was tightly twisted at one end. Examination of the excreta showed that most of the food consisted of ants, but the remains of a few beetles, two flies and one caterpillar were also present. Feeding takes place about every hour while the young are small, but when they are about a week old the interval is increased to around two hours which is maintained for the rest of the period in the nest.

On May 15, 1939, when the young of the first nest studied were five days old, I watched the male return to the nest after I had replaced them. He fed them, brooded about ten minutes and then left. I again removed the young and reweighed them, finding that apparently only one young had been fed and this one had received 6.3 grams of food. Of course there is a chance for error here, in that one or both of the other birds may have received food and defecated a sac of equal weight, but this is unlikely.

The method of feeding the young is that of regurgitation. The adult inserts its long bill into the throat of the young, and as the young sucks and jerks its head the parent regurgitates the food, which is swallowed by the baby. This method of feeding continues throughout the nesting period and for some time after the young have left the nest.

Our observations agree completely with the graphic description by Bent (1939, p. 180) of the method of feeding the young when they are still at the bottom of the hole: "The incoming bird hops to the hole, perches on the ridge of the entrance passageway, and then swings inward and downward, at the same time elevating the posterior part of its body until the tail presses against the outer upper rim of the hole. In this position evidently the parent's bill meets those of the nestlings. This attitude is maintained often for much as a minute and while it is maintained the body of the bird may be seen to shake convulsively—plainly indicating that regurgitation is in progress." Later when the young met the parent at the entrance, the adult sometimes pushed the young down into the hole, for feeding, or else the adult clung somewhat to the side of the hole and the young reached to that side for the feeding process.

During the first two weeks, the parent frequently broods the young following feeding, even remaining until the other parent returns. Later, brooding may be omitted entirely, and the observer may arrive at the nest to find both parents gone, the young possibly hanging part way out of the hole, watching the surroundings.

Bent (1939, p. 180) states that it is probable that the excrement of the young is carried out and dropped, or else is eaten in the early stages of nesting. I agree, in that no signs of excreta were ever found in the nest. On many occasions we saw the parents carrying it out, but only after the fifth day. The feces may therefore be eaten the first few days, carried out and dropped later when the young are somewhat larger.

The reaction of the parents to the presence of humans around the nest varied from time to time. Generalizations can not be drawn from these cases, for it must be remembered that the pairs under observation in this study had had plenty of opportunity to become accustomed to our presence and might have behaved differently had we suddenly turned up for the first time during the nesting period.

This pair often flew away as we approached, calling as they flew. At other times they remained near the nest, silently watching the intruder from behind the trunk of a large tree. As the young became older the adults grew braver or showed a stronger drive to remain near the nest and protect it, even coming on the nest tree while the observer stood beneath it. Upon one occasion the male of this pair seemed to be trying to lead the observer away from the vicinity, flying short distances, calling until I was close, flying another short distance, calling, until I was some distance from the nest.

On the 12th day of work with the 1941 nest, a quite unusual event occurred. The male landed on the nest tree while the young were being removed for the usual daily observations, and attacked my husband quite viciously, landing repeated blows on his hand that was against the tree trunk. Dr. Hoyt finally grasped the woodpecker's feet and tossed it into the air, only to have it return to the attack. This was repeated on the 13th and 14th days and motion pictures of the attack were taken by A. A. Allen and by the writer. After that, care was taken to avoid inciting the male to attack, because of the risk of desertion.

Upon several occasions the first flight of the young bird from the nest was observed. It was of particular interest that the bird was able to sustain flight for several hundred feet, losing altitude slowly, and then climbing slowly up a tree trunk. On one occasion, in 1942, the youngster was caught and banded before it climbed. Considering the fact that up to four young have been confined in a relatively crowded space in a hole in a tree, without opportunity for exercising their wings, it is amazing that they can fly so well immediately.

For the first few days, they remain fairly close to the nest. In 1939 it was noted that most of the time was spent in flying from one tree-top to another and calling for food. When they called, the parents would answer with a low, nasal cluck call, at which the young responded by calling more loudly and flying in the general direction of the parents, who soon joined them with food. Feeding was by the same regurgitation method as during the time in the nest.

Observations seem to indicate that the parents show the young how to locate food beneath the bark, or in holes. Upon several occasions the parent bird was seen digging a hole, and then the youngster worked over the hole looking for food, while the parent watched. The family group seems to stay more or less together at least into September, and perhaps later.

In regard to sex ratio, an interesting situation prevailed, although the data are too few to generalize or draw conclusions. The nest contents of four nests were carefully studied, over a ten year interval. In each case four eggs were laid, three of which hatched. In three of these nests, two of the surviving young birds were females and the third a male. Having numbered the eggs and having marked the young birds after hatching, it was noted that the last egg to hatch, presumably the last to be laid, was that from which the male developed. In other words, of the three young birds in the nest the smallest, lightest and most retarded has in each case been the male. In one of these nests this smallest bird died before leaving the nest. The fourth nest not included in the above remarks also contained three young birds, but the youngest died at seven days of age, just too young to determine the sex. The other two were females.

Incidental Observations

Published references to the flight of this species often state that the pileated flies in a straight line, without the undulation shown by other woodpeckers. This is usually the case, but our notes indicate that there was sometimes a definite undulation to the flight as they came to the nest or the roost.

I have been unable to find any reference to pileateds bathing in the wild, nor have I heard of anyone who has observed this. Our captive bird taken from the nest on the 26th day in 1941 and kept until her death in 1950 (J. S. Y. Hoyt 1950b) often bathed in a basin, soaking herself completely. Also, when a glass was suspended in one corner

of the cage, for drinking water, she was observed dozens of times in the process of getting a regular shower bath—by pushing the glass back and forth and ducking under the water which spilled out. In this manner she would empty the glass and become completely soaked, then preen, and spread her wings while she dried.

Drinking has rarely been observed in the wild, which may indicate that they get moisture from insect fare, or that they drink from crevices in trees. The captive bird would dip her bill into the water, throw her head back and swallow several times. This might be repeated up to thirty times.

Parasites

On the eleventh day of the 1939 nest, ectoparasites were noted on the three young, which were identified by Mr. Scudder of the Entomology Department at Cornell as members of the Phoridae family or humpbacked flies. These little flies were running through the feather tracts of the wing but seemed to collect especially in the fold of the skin at the joint of the wing. They did not seem to bother the young birds. On the fourteenth day of the study of the developing young of the 1941 nest, the same kind of flies were found on these birds. As many as could be gathered were collected but many escaped among the feather tracts. By the sixteenth day none could be found on the birds nor gathered from the chips in the bottom of the nest. We have questioned others who have handled young pileateds, but have had no reports of these parasites being found. It is hoped that future observers will look for parasites on the young.

Economic Importance

There are so many wood-boring insects in our forests that were it not for the important role played by the pileated woodpecker, and others of the family, man would be in a serious situation in respect to control of insect damage. The pileated leads all the others in its ability to handle certain types of insects and in the numbers eaten. Many people have commented on the habit of these birds of staying with an infected tree until they have rid the tree of its enemies. This habit alone is of the greatest importance, for it prevents the further infection of trees in a vicinity as well as giving the infected tree a chance to live. Of course there are cases where the birds have dug many holes in a tree and the tree has later died. Casual observers are likely to condemn the birds for this, but the truth of the matter is that the trees were already doomed if the woodpecker needed to do so much work on them to rid them of insects.

At present as mentioned earlier pileated woodpeckers are the subject of a serious study by utility companies, because of damage done to poles in remote areas. Although some quite ridiculous statements have been made, it is noteworthy that a careful and scientific examination of the facts is being made at Pennsylvania State University. It should be pointed out, I feel, that in the remote areas where poles are attacked, wide areas have been cleared on either side of the power lines, and many diseased trees cut down. Carpenter ants and other insects would no doubt be inspired to attack new poles in the absence of much of their former fare. Also, I am told that examination of creosoted poles sometimes shows that the centers have not been reached by the creosote and it is the heart wood which is invaded by carpenter ants, working from the ground up, with no external evidence of their attack. In such cases, the woodpeckers are merely ridding the poles of insects which would eventually destroy the poles. Getting food is serious enough business for pileateds in late fall and winter that they will not waste time and energy digging holes for fun.

The Status of the Species

The pileated woodpecker has saved itself from extinction by its ability to adapt itself to the advance of civilization. For years this bird was on the rapid decrease and it looked as if there were little or no hope for it. As observers soon noted in the field, the birds were holding their own for a time and then the number started increasing until at present there are many regions that can boast a few pairs of these magnificent birds where a few years ago none could be found. This ability to withstand the advance of civilization manifests itself in the fact that the birds may now be found in woodlots near farms and even near cities in some instances or within the borders of smaller towns. They can now live in second growth and among smaller trees than before, and are willing to cross open country from one small woodlot to another. This is of great importance to the future of such a bird as the pileated woodpecker, for instead of having to retreat before the woodsmen they can now live among the conditions caused by the foresters. Pileateds are even beginning to visit bird-feeding stations in a few instances and this is being chronicled elsewhere.

Fortunately the pileated woodpecker has few enemies, except man. George M. Sutton wrote (1930, p. 214) that in Pennsylvania the duck hawk appeared to be the chief and perhaps the only

natural enemy of this woodpecker. Bent (1939, p. 188) quotes R. B. Simpson as having found one indication of a wildcat catching a pileated. Dr. William Rhein of Harrisburg, Pennsylvania photographed a remarkable incident of a pilot black snake (*Elaphe obsoleta*) climbing a tree and attempting to eat the young pileateds in a nest. The birds were rescued by Dr. Rhein.

Unfortunately many pileateds are shot each year, some because of a mistaken idea that they are damaging timber, a very few through wrong identification but most of them through curiosity. The woodpeckers were once used as food to a small extent, according to old records, and probably also were used for decoration by Indians.

Education is still needed so that the hunter will respect this bird and not shoot it. Its value to our forests is immeasurable and while it is increasing in numbers it has by no means reached the point where it can stand any real campaign against it for any reason. I cannot conclude without pointing out also what might be termed the esthetic value of the species. Denizen of deep forests and swampy areas, never tame, a glimpse of it remains a thrill for most who see it for the first time or the thousandth.

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THE EFFECTS OF ACIDITY ON THE DEVELOPMENT AND HATCHING OF NEW JERSEY FROGS[1]

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Introduction

The role of hydrogen-ion concentration or pH as a factor in the ecology of fresh water organisms is the subject of an extensive literature reviewed by Allee *et al.* (1949) and Welch (1952). Comparatively little work has been done, however, to indicate the possible effects of this factor on the breeding cycle of tailless amphibians.

The present investigation was initiated in connection with a study of the distribution of frogs and toads in the pine barrens of southern New Jersey. The barrens are covered by a basically pitch pine (*Pinus rigida*) forest, intermingled with bogs dominated by southern white cedar (*Chamaecyparis thyoides*). The area includes a considerable portion of the eastern region of southern New Jersey, extending from southern Monmouth County to northern Cape May County. It originally was about 75 miles long and 35 miles wide (Harshberger, 1916), but has undergone great change through the years and the barrens are now much more limited in extent.

In variety of species the anuran population of the barrens is markedly restricted in comparison to that of adjacent areas. In the barrens only

[1] We wish to thank Dr. Benjamin Sonnenblich of Rutgers University for reading the manuscript and giving critical help in its composition.

three species of the eleven common in the surrounding area have large populations: the southern leopard frog (*Rana pipiens sphenocephala*), the green frog (*Rana clamitans melanota*), and Fowler's toad (*Bufo woodhousei fowleri*). The chorus frog (*Pseudacris nigrita kalmi*), the wood frog (*Rana sylvatica sylvatica*), and less frequently the common tree frog (*Hyla versicolor versicolor*) breed in altered situations such as flooded fields and gravel pits within the barrens area. This is also essentially true of the spring peeper (*Hyla crucifer crucifer*), although records of vocalizing individuals suggest a wider distribution for this species. The spadefoot toad (*Scaphiopus holbrooki holbrooki*) has been recorded from transient pools and gravel pits from a number of localities. The pickerel frog (*Rana palustris*) and the cricket frog (*Acris gryllus crepitans*) have been taken only from peripheral and partly intrusive situations. The bull frog (*Rana catesbeiana*) appears to be completely absent from the area although many of the lakes and ponds would appear to offer suitable habitats.

Two species are pretty much restricted in New Jersey to this area or its edges; the carpenter frog (*Rana virgatipes*) and the pine barrens tree frog (*Hyla andersoni*). The latter species also has a small population in the pine "island" in Middlesex County. Both *Rana virgatipes* and *Hyla andersoni* have a disjunct distribution south of New Jersey, *Hyla andersoni* being known from only two areas outside the state.

Rana virgatipes usually inhabits the larger rivers, artificial lakes, and flooded cranberry bogs where there is floating vegetation, usually mats of sphagnum moss. Its associates are generally *Rana p. sphenocephala, Rana c. melanota,* and, in its breeding season, *Bufo w. fowleri.*

Hyla andersoni breeds in small acid pools or slow-moving streams, usually surrounded by heavy shrub growth; *Rana virgatipes* may occur in the vicinity, but it normally inhabits a different habitat.

The distributional data suggest that factors exist limiting the occurrence of various species in the area. Since strongly acid conditions seem to be characteristic of most breeding habitats in the pine barrens, the possible effect of low pH on the breeding cycle of the various species is a factor to be considered. This factor was investigated through laboratory experiments supplemented by field observations.

Preliminary Considerations

In natural aquatic environments pH is involved in various physical and chemical reactions. These relationships are complex and make it difficult to evaluate the specific importance of pH in problems of animal ecology. Under laboratory conditions the variables may be more completely controlled. In formulating a working hypothesis, a number of ways in which pH might exercise a limiting effect on the breeding cycle of the Anura were considered.

Some of these concern the fertilization process. For example, pH is known to have importance in determining optimum conditions for sperm activity in many animals. In addition, there are possible effects on the activity of gamones such as fertilizin (Nelson 1953; Brachet 1950) that are important in the reactions of sperm and eggs.

The fertilized eggs and embryos also are subject to physico-chemical factors in the aquatic environment. The egg membranes are not completely impermeable and lethal effects might occur from the toxicity of the cations of specific acids, or simply through the degree of acidity alone. Such effects could involve embryonic processes or the control of gaseous, water, and ionic exchanges between the embryo and the external environment.

Another point at which pH might limit embryonic development involves the hatching process. It is fairly well established that anuran embryos hatch by liberating a protease that attacks the egg membranes and permits the young to escape (Noble 1926; Needham 1942). The role of pH in moderating enzyme activity is well known and, were the hatching proteases inactivated by low pH solutions, this could be an important limiting effect. The above considerations, we may note, do not exhaust the possibilities for pH effects on the breeding cycle of anurans but they do at least provide a basis for the design of experiments.

Materials and Methods

Solutions of several types were used. Newark tap water has been found entirely satisfactory for culturing anuran embryos and larvae and during several seasons we have successfully reared nearly all of the local species in this medium. Tap water was, therefore, used as the principal control medium. The pH of this water varied from 6.9 to 7.8 during the two working seasons. Allee *et al.* (1950) raised objections to the use of standard buffer solutions in ecological experiments and such solutions were avoided. Tap water was acidified by adding hydrochloric acid. Ellis (1937) demonstrated that the tolerance of fresh water fish for different acids varied widely, with hydrochloric acid occupying a middle position among the acids

on his scale of lethality. In order to take this variation into consideration duplicate experiments were performed with bog water from the pine barrens.

Bog water was secured in five gallon carboys from a pool at Speedwell, Burlington County, New Jersey. This pool is a breeding locality for four of the "characteristic" pine barren anurans and supports a wealth of invertebrate life. The pH of water from different parts of the pool, tested in the field at different seasons and at different times of the day varied from 3.9 to 4.3. When secured and stored in a large volume this water held its original pH value for several weeks or longer. The pH of the bog water was altered, towards neutrality, by the addition of sodium hydroxide. The hydrochloric acid and sodium hydroxide solutions used to modify the pH of test media were obtained by diluting M/5 solutions (LaMotte special stock for the preparation of buffer solutions) with four parts of distilled water. The quantity of reagent required to adjust the test media represented an increase in the molar concentration of less than .05 grams/100cc of solution.

Unbuffered solutions are essentially unstable. The ability of test solutions to hold an established pH value varies depending on the volume used, the area of contact of the solution with the air or the container, and the number of eggs used. It was possible to maintain solutions within about 0.1 pH unit of the original value for 24 hours or longer allowing about 15 eggs to 600 cc of solution in a quart-size glass jar with a cap placed loosely over the mouth. Such solutions were changed daily and the pH tested before discarding. Colorimetric determination of pH was made with a LaMotte Block Comparator using the following indicators and standards for the ranges shown: Bromthymol Blue, pH 7.6-6.0; Methyl Red, pH 6.0-4.4; Bromcresol Green, pH 5.4-3.8; and LaMotte Yellow, pH 4.2-2.6. The standards are in 0.2 pH intervals and permit estimates to 0.1 pH. The design of the comparator provides a means of correcting for the natural color of field samples.

Eggs were obtained either freshly laid in the field, or from pairs mated in the laboratory, or artificially by stripping ripe eggs into a sperm suspension. Eleven different species were studied. In each experiment lots of about 15 eggs were taken from a single spawning. One lot was placed in 600 cc of tap water, the others in acidified solutions usually regulated at 0.2 pH intervals. All of the containers used in any one experiment were of the same size and shape and all of the jars were kept together under equivalent conditions of light and temperature. The numbers used in this report to indicate developmental stages of embryos are those figured by Rugh (1951).

Characteristics of Pine Barren Water

The natural water in typical sphagnaceous pine barren habitats is strongly acid; the average pH of pine barren peat deposits is 4.0 with a range of 2.0-5.0 (Little 1950). The mean pH of 25 observations made by us in different parts of the barrens is 4.4; the range is 3.6-5.2. These were principally surface water samples from bogs, swamps, streams, and lakes at eighteen different localities in Atlantic, Burlington, Cape May, Cumberland, Gloucester, Monmouth, and Ocean counties. Tests were made between 11 a.m. and 12:15 a.m. from late February through late June. Repeat tests at a few localities, such as Speedwell, Burlington County, show some variation at different times and in different parts of the study site. However, there is no clear evidence of pronounced seasonal or diurnal trends in changing pH values.

The specific cause of the high acidity of the pine barren water has not been determined. The acidity of bogs in general has been attributed to "organic acids" (Welch 1952: 390).

There is no indication that carbonic acid is a major factor. The pH of water from Speedwell was unaffected by aeration or by boiling for a short period. Prolonged boiling, however, with extreme reduction in volume, lowered the pH value. A sample of 1000 cc was boiled down to 15 cc, diluted with an equal volume of distilled water, filtered, and the pH tested; the value before boiling was 4.3 and after boiling 2.7.

Collins and Howard (1927) and Love (1950) present data on the quality of surface waters in New Jersey. The water in streams draining the barrens is soft, being very low in dissolved calcium, magnesium, and bicarbonate in contrast to water samples from other parts of the state. Since these components are usually important in natural buffer systems, an attempt was made to determine the effectiveness of buffers in Speedwell water by testing the pH of progressively more dilute solutions of bog water. The initial, undiluted sample had a pH of 4.1. With distilled water in the following ratios (upper figure equals bog water), the pH changed as indicated; 6/1-pH 4.2; 4/1-pH 4.4; 2/1-pH 4.6. The bog water would appear to be weakly buffered.

In summary, the natural water in breeding situations in the pine barrens may be characterized as strongly "tea" colored but usually clear, with low dissolved mineral content, weakly buffered,

and strongly acid. The acidity is probably due to organic acids and is very likely partly derived from the sphagnum associated with these localities.

The water is transient pools and gravel pits in the barrens is much less acid than that in the sphagnaceous localities. Ten samples from five different counties gave a mean pH of 6.3 and a range of 5.5-6.6. These were situations utilized for breedings by *Pseudacris n. kalmi, Hyla c. crucifer, Rana s. sylvatica* and *Bufo w. fowleri.* The mean pH of eleven samples from localities in northern New Jersey is 7.8 and the range is 6.6-9.5. The highest values were obtained from breeding pools in the Kittatinny Limestone formation in Sussex County.

Terminology of Embryonic Responses

We shall describe the reactions of anuran embryos to low pH broadly in terms of three levels of response. (A) The pH value associated with irreversible cessation of normal development is termed the *lethal* value. Such solutions kill 85% or more of the embryos within a period of a few hours. (B) Solutions with somewhat higher pH values are identified with a *critical pH range.* Solutions within the critical pH range cause high mortality among the exposed embryos but the effects appear to be more complex and less direct than in the preceding category. (C) Finally, there is a pH value near the upper limit of the critical pH range which we term the *minimum limiting pH* value. Exposure to such solutions permits most (50% or more) of the embryos to develop into normal hatchlings.

The responses of the species studied are indicated graphically in Figure 1. A discussion of these responses follows. Most of our work was performed with ranges (B) and (C) as defined above. Responses to bog water and tap water acidified with hydrochloric acid were equivalent at similar pH values and the two types of media will usually not be distinguished in the discussions that follow.

Lethals

Lethal values, usng hydrochloric acid in tap water, varied from a pH below, 3.5 for *Rana virgatipes* to 4.0-4.1 for *Acris g. crepitans. Rana virgatipes* was tested with a tannic acid-tap water solution at pH 3.9-4.0; the exposure was lethal.

Critical pH Range

The critical pH range for the species tested varied from pH 3.6-3.8 for *Rana virgatipes* to about pH 4.2-4.6 for *Acris,* the upper figures in each case indicating approximately the *Minimum Limiting pH.* Preliminary experiments indicated that in certain pH solutions embryonic development continued through to the hatching stage but most of the embryos either failed to escape from the egg membranes or were abnormal at hatching. In this type of response the eggs failed to swell in the later stages and it is pertinent to consider this effect further. Krishna (1953) observed a *shrinkage* of the yolk of trout eggs in acid solutions. Krogh (1939) states that a slow flow of water into the perivitelline space in frog eggs is necessary for normal development. Aside from the slight initial absorption of water to produce the perivitelline space the major increase in the size of this space comes after Stage 12 (late gastrula). Measurements of the diameter of normal eggs (area inclosed by the perivitelline membrane) were made in experiments involving five of the different species. From the late gastrula stage (Stage 12) to the pre-hatching stages (Stage 18-20), the diameter of the egg increased 1.7-2.1 times the original measurement in groups reared in tap water. Eggs exposed to pH values near the lower limit of the critical pH range (Fig. 1) increased in diameter by 1.0 (no increase) to 1.3 times the original diameter.

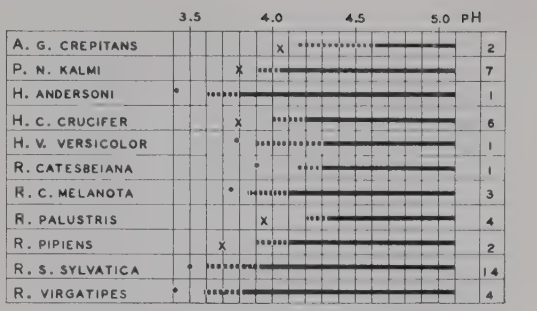

Fig. 1. Responses of anuran embryos to tap water-HCl solutions. The solid line indicates the tolerable range below pH 5.1; the broken line indicates the critical pH range; "X's" indicate observed lethals; solid dots indicate estimated lethals. The numbers in the right hand column are the number of experiments made with each species.

Groups of eggs exposed to solutions near the lower limit of the critical pH range continued development in most instances. Occasionally, the rate of development was diminished and hatching was delayed. Observation under a low power binocular microscope revealed that the embryos were severely restricted in their movements and in extreme cases were tightly curled in the later stages of development. In normal eggs, the Stage 18-20 embryos have sufficient room for muscular activity and such activity increases markedly as the time for hatching approches. When hatching

did occur in strongly acid cultures, the young were usually bent or arched, locomotion was abnormal, and the rate of activity was reduced.

Holtfreter (1943) gave the opinion that the size of the perivitelline space is dependent on the osmotic pressure gradient across the egg membranes. We performed a number of experiments to compare embryonic responses to salt solutions with the effects of solutions at low pH. Standard Holtfreter solution (0.385 grams per 100 cc of water) was diluted with distilled water to give salt concentrations of 0.150, 0.250, and 0.350 grams per 100 cc of water at pH 7.0 ± 0.5. Distilled water was also used in some tests. The species tested include *Pseudacris n. kalmi, Hyla c. crucifer, Rana s. sylvatica, Rana palustris, Rana pipiens,* and *Rana virgatipes.* The purpose of these tests was not to establish tolerance limits but to provide a qualitative picture of the effects produced. The responses varied among the different species. The two hylids were adversely affected by the 0.150 concentration and both the hylids and *Rana s. sylvatica* were adversely affected by the 0.250 concentration. A few embryos of the other ranids hatched normally in the 0.250 solution but only *Rana virgatipes* showed any normal development in the 0.350 solution.

The eggs of four species were tested with distilled water and most of these developed normally and hatched. Hatching in the salt solutions was delayed somewhat and the hatchlings were smaller in size. With salt in concentrations of 0.250 or more the eggs were smaller (perivitelline space with less absorbed water). In tap water, distilled water, and in the 0.150 salt concentration medium, the diameter of the perivitelline capsule at the end of embryonic development was as much as 2.0 times greater than at the gastrula stage (Stage 12). Deleterious effects associated with exposure to salt solutions include morphological abnormalities similar to those of embryos hatched from strongly acid solutions, *i.e.* the hatchlings were bent or arched and somewhat runted. Locomotion was abnormal and the rate of activity reduced.

In view of the similarity of the effects of salt solutions and of low pH solutions it seems reasonable to suspect that the observed deleterious effects on embryonic development may be due, in part at least, to mechanical pressure on the embryos. Such an effect would prove to be a limiting factor by inhibiting the ability of species to breed successfully in strongly acid environments. Our observations do not reveal the extent or quality of other and possibly differential effects of the two types of media. With the data available it is possible to speculate that continuous exposure to low pH solutions during embryonic development may cause some alteration of the egg membranes that results in abnormal osmotic regulation.

In order to determine whether the effects of low pH solutions are partly or wholly reversible, two types of supplementary experiment were performed with *Rana sylvatica* eggs. One procedure involved placing eggs in a solution that would restrict normal hatching to a minimum; small lots of eggs at increasingly advanced levels of development were serially removed to tap water. The second procedure involved transferring eggs at various growth stages from tap water to low pH solutions.

With respect to the first procedure a group of *R. sylvatica* eggs, divided in small lots, was placed in water at pH 3.5-3.7 when the embryos were in Stage 9 (late blastula). As development proceeded lots of 10-17 eggs were removed at Stages 12 (late gastrula), 14 (neural fold), 16 (neural tube) and 19 (heart beat) and placed in tap water. Of the eggs that remained in acid water throughout the experiment approximately 50% failed to hatch and the remaining 50% hatched with some delay and were morphologically abnormal to a greater or lesser extent. Of 11 eggs removed at Stage 12, 9 hatched normally; of 17 eggs removed at Stage 14, 4 hatched but were abnormal and 6 hatched normally; of 10 eggs removed at Stage 16, 6 hatched but were abnormal; of 15 eggs removed at Stage 19, 11 hatched but were abnormal.

In the complementary experiment, a group of eggs, divided in small lots, was placed in tap water at Stage 11. As development proceeded lots of 10-15 eggs were removed at Stage 12, 15 (rotation) and 19 to hydrochloric acid-tap water solutions at pH 3.6-3.7. Of 11 eggs transferred at Stage 12, 8 hatched but were abnormal; of 10 eggs transferred at Stage 15, 9 hatched normally; of 15 eggs transferred at Stage 19, 15 hatched normally. The eggs transferred at later stages lost some water from the perivitelline space. The slight resulting constriction did not cause deformities in the hatchlings but some delay in hatching was observed.

It is important to note, as indicated in the latter experiment, that the hatching proteases of *Rana sylvatica* were apparently operative at very low pH. The evincing of deleterious effects with low pH solutions may thus require continuous or prolonged exposures. The possibility should be considered that low pH may restrict hatching through some alteration of the egg membranes making them less susceptible to the effect of the hatching

proteases rather than by inactivation of the enzymes. In this connection, it may be noted that the jelly membranes of eggs in such solutions develop a turbid appearance that contrasts with the usually clear jelly coating of eggs cultured in clean water. The jelly coats normally change during development, becoming less resilient in the later stages. Eggs in acid water retain a firmer consistency. In instances where full-term embryos did not hatch, wriggling activities failed to effect an escape from the egg membranes. Such embryos died within 24-48 hours after reaching the developmental stage at which hatching should have taken place.

Larval Tolerances

Freshly hatched larvae of *Rana palustris* were maintained for two days at pH 3.7-3.8 and freshly hatched larvae of *Pseudacris* were kept for four days at pH 3.8-3.9. No ill effects were observed. These results suggest that anuran larvae may have a greater resistance to low pH than do the embryos.

Noble and Noble (1923) reported that they were unable to rear tadpoles of *Hyla andersoni* in tap water and concluded that "bog water is essential to normal development." Such a requirement would explain the restriction of this species to pine barrens habitats or to equivalent situations elsewhere. During 1954, however, we successfully raised *Hyla andersoni* embryos and larvae through metamorphosis in Newark tap water on several occasions. Also, larvae at various stages of development were secured in the field and transferred to tap water where normal development was completed. *Rana virgatipes* embryos were also cultured in this medium and several larvae were kept for periods of nine months or more in tap water aquaria. On another occasion, a lot of *Rana virgatipes* embryos was placed just prior to hatching in water from a limestone pool at Swartswood Lake, Sussex County, New Jersey. The medium had no ill effects on the embryos although the pH of this water was 9.2. Bog water, therefore, may not be essential for normal embryonic or larval development. The restricted distribution of the two endemic pine barren species may be due to the habitat requirements of the adults, to a reduced ecological adaptability or to other factors sometimes contained in the concept of "species senility" (Cain 1944). In view of the pronounced disjunct distribution of these two forms, as mentioned earlier, it may be important to consider historical factors as well as current conditions in any attempt to explain their present distribution.

Little information relative to the effects of low pH on fertilization was obtained due to the difficulty in maintaining stable solutions during the experimental period. In two experiments with clasping pairs of *H. c. crucifer* in bog water at pH 4.2-4.5, the frequency of eggs showing cleavage among those laid was 47% and 100%. We cannot account at this time for this disparity. In a single experiment with a pair of *Pseudacris* in bog water at pH 4.7 the precentage of eggs fertilized was close to 100%.

Summary and Conclusions

1. The anuran populations of the New Jersey pine barrens are restricted in variety of species in comparison with those of adjacent areas. *Rana virgatipes* and *Hyla andersoni* are two characteristics species found in typical sphagnaceous barren habitats; *Rana pipiens sphenocephala, Rana clamitans melanota* and *Bufo w. fowleri* are their normal associates. Other New Jersey anurans breed in the barrens in intrusive, usually non-sphagnaceous, situations such as grassy pools and gravel pits. *Rana palustris, Rana catesbeiana* and *Acris g. crepitans* are generally absent from the barrens.

2. The water in typical sphagnaceous breeding habitats in the pine barrens is clear but strongly "tea" colored, weakly buffered, and with low dissolved mineral content. It is acid with an average pH between 4.0 and 4.3. The observed pH range was 3.6-5.2. The pH range of grassy pools and gravel pits in intrusive areas was 5.5-6.6.

3. Embryonic tolerances for acid water varied in the eleven species tested. A pH of 3.8 or lower in bog water or hydrochloric acid-tap water solutions results in some abnormal development in *Rana virgatipes* while a pH of 4.2-4.6 has a similar effect on *Acris*. Deleterious effects on embryonic development are characterized by a failure of the perivitelline space to absorb normal quantities of water following the completion of embryonic Stage 12. This restriction apparently subjects the embryo to mechanical pressure resulting in morphological and behavioral abnormalities. Exposure to salt concentrations of 0.150-0.350 grams per 100 cc results in similar abnormalities. It is possible that deleterious effects associated with exposure to the acid solutions employed may have been due to alterations in the properties of the egg coats, interfering with normal osmotic control and responses to hatching enzymes.

4. The acidity of bog water in the New Jersey

pine barrens may be a limiting factor in the distribution of anurans. *Rana virgatipes* and *Hyla andersoni* embryos tolerate more strongly acid solutions than any of the other species tested. *Rana palustris* and *Acris g. crepitans* have the least tolerance to such conditions and these species are practically absent from unaltered pine barrens habitats. Seven of the eleven species tested require bog water or tap water acidified with hydrocloric acid at at a pH of 4.1 or higher for normal development.

5. *Hyla c. crucifer* is capable of spawning successfully in bog water at a pH of 4.2-4.5. *Pseudacris* is able to spawn in bog water at pH 4.7, or perhaps even lower.

6. We recognize the probability that additional factors are involved in limiting the distribution of local anurans in the barrens. In fact, it is likely that none of the species is either restricted to or excluded from the pine barrens by the pH factor alone. It is possible that for some species, however, pH may have some significance since many of the bogs and swamps are too acid for normal embryonic development to occur. Other physical or chemical factors in the bog water, at present unknown, may have deleterious effects on the embryos, the larvae, or on the fertilization process itself.

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ECOLOGICAL STUDIES OF THE ARTHROPODS ASSOCIATED WITH CERTAIN DECAYING MATERIALS IN FOUR HABITATS

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Introduction

When plants and animals in any habitat die, they are set upon by saprophagous organisms. During decay there is a succession of organisms associated with the decaying material, that is, the number and kind of associated organisms change as decay proceeds. The succession of organisms is influenced by variations in vegetation and microclimate. This influence is chiefly through effects on the course of decay and the character of the fauna of the area. Since a great diversity of vegetational types (and a corresponding diversity of microclimates) may occur in an area of a few acres, the animals associated with similar decaying materials in adjacent habitats may be quite different.

Many studies have been made on the arthropods associated with decaying substances in single habitats, but in only a few cases have direct comparisons of different habitats been made and most of these are in the nature of casual observations. Jaques (1915) found that Coleoptera are most active at fish "in damp shaded places and resort to fish of the sun-heated beach only of necessity."

Park (1931) made some general observations on the effect of moisture upon the beetles associated with fungi. Walsh (1931, 1933) set carrion-baited traps in "wood" and "moor" and recorded the catch. Kaufman (1937) found that of two carrion-baited traps in his garden, the one in the moister situation was the more productive. Savely (1939) studied the successions of animals in oak and pine logs and investigated the microclimate within the decaying logs. Mohr (1943) made an excellent study of the arthropods associated with cattle dung in open pastures. He states that the environment in which the dung is dropped has a profound effect upon its fauna but presents no detailed comparison of differing habitats. Reed (1953) investigated differences in the arthropods associated with dog carcasses in wooded areas and in open pastures.

Since comparative studies are so few, this study was undertaken to determine what sorts of similarities and differences may occur in the arthropods associated with decaying materials in different habitats in the same area. It involves (1) the description of four local habitats in regard to certain aspects of their vegetation and microclimate and (2) the analysis of arthropod collections from three organic materials placed as baits in each of the four habitats.

The writer is indebted to Dr. Arthur C. Cole, Jr. and Dr. Royal E. Shanks for numerous suggestions in connection with the planning of this study, and to Dr. Donald J. Borror and Dr. John N. Wolfe for advice and criticism in the completion of the project and in the preparation of this manuscript. The following systematists contributed freely of their time and skill in the identification of the various taxonomic groups encountered in this study: E. W. Baker, Acarina; B. D. Burks, Hymenoptera; O. L. Cartwright, Scarabaeidae; R. V. Chamberlin, Myriapoda; E. A. Chapin, Coleoptera; A. C. Cole, Jr., Formicidae; R. H. Foote, Diptera; C. A. Frost, Coleoptera; W. J. Gertsch, Araneae; L. R. Gillogly, Nitidulidae; C. J. Goodnight, Phalangida; J. N. Knull, Coleoptera; K. V. Krombein, Hymenoptera; C. F. W. Muesebeck, Hymenoptera; Alvah Peterson, immature insects; C. W. Sabrosky, Diptera; M. W. Sanderson, Staphylinidae; R. E. Shanks, flowering plants; A. J. Sharp, flowering plants; E. L. Sleeper, Curculionidae; W. C. Stehr, Carabidae; A. Stone, Diptera; E. S. Thomas, Orthoptera; J. K. Underwood, grasses and sedges; L. M. Walkley, Ichneumonidae; L. H. Weld, Hymenoptera; R. L. Wenzel, Histeridae; W. W. Wirth, Diptera; D. L. Wray, Collembola; and F. N. Young, Hydrophilidae.

The Habitats Studied

This study is based upon field work done from June 24 until August 6, 1952, in four habitats of differing vegetation about eight miles southeast of Camden, Tennessee. Figure 1 shows the exact locations and the topographic relationships of the habitats. The following general descriptions of the vegetation in each of the selected habitats were substantiated by sampling.

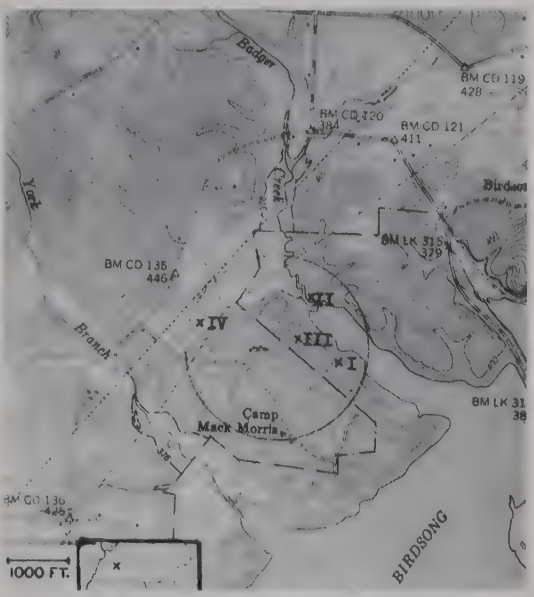

FIG. 1. Topographic map of study area: 35° 58′ N Lat., 88° 04′ W Long. Habitats are indicated by small *x*'s within circle. The X on the insert map of Tennessee indicates the general location of the area.

Habitat I was located near the mouth of a valley draining northeastward. The relatively level valley floor was locally interrupted by shallow drainage channels. A rich deciduous forest dominated by red maple (*Acer rubrum*) and sweet gum (*Liquidambar styraciflua*) formed a tree canopy with a coverage of about 80%. *Quercus velutina*, *Quercus alba*, and *Nyssa sylvatica* were important subdominant canopy species. Commercially valuable trees had been removed from the area about twenty years before. Hazelnut (*Corylus americana*) and *Euonymus americanus*, together with many young trees, formed a well-developed shrub layer. Ground cover was sparse but varied.

Habitat II was situated in the flood plain of Badger Creek, thirty yards north of the creek. That the area was periodically flooded was evidenced by drift washed against the bases of trees; shallow drainage channels were present. About twenty yards north of the area, the ground rose

slightly above the level of flooding. A marshy area associated with Kentucky Lake began thirty yards east. The forest in Habitat II was a park-like stand of large deciduous trees with little shrub layer and few small trees. Six species were prominent in the canopy—*Quercus falcata, Quercus alba, Liquidambar styraciflua, Carya ovata, Nyssa sylvatica,* and *Liriodendron tulipifera.* Hornbeam (*Carpinus caroliniana*) formed a relatively continuous tree understory, even predominating over the canopy species in basal area (about 20%) and in number of stems (about 45%). There was no evidence of lumbering. Grasses and sedges were markedly dominant in the sparse ground cover.

Habitat III was on a SE-NW ridge approximately forty yards wide and with steep sides. The forest canopy in Habitat III was quite broken, having a coverage of only about 30%. Post oak (*Quercus stellata*) and white oak (*Quercus alba*) were the dominants. *Quercus marilandica, Quercus coccinea, Quercus velutina,* and *Carya glabra* were important subdominants. The area had evidently been lumbered at the same time as Habitat I. The shrub layer was well-developed and quite dense in some places, *Vaccinium stamineum* being the dominant shrub. The herbaceous layer was extremely sparse, with poison ivy (*Rhus radicans*) the most conspicuous component.

Habitat IV was an abandoned field with rocky soil twenty yards from the top of a hill, on a south-facing slope. A wooded draw was fifty yards south. The area had been planted with pines (*Pinus rigida*) in the fall of 1946. However, the pines were too small to appreciably influence the microclimate, and a fire in the spring of the year of the study (1952) had resulted in the death of many of the trees. The ground cover was relatively uniform but covered only about 20% of the soil. *Andropogon virginicus* was dominant.

Techniques

The arthropods studied were trapped on three materials—cornmeal, cantaloupe, and fish. In each habitat a circle of twelve traps, each ten feet (3.05 m) from its nearest neighbor, was laid out (Fig. 2). The traps were No. 10 (gallon-size) tin cans buried flush with the soil surface. The mouths of the traps were covered with foot-square pieces of galvanized metal resting on stones about two inches in diameter. The cans were washed thoroughly before burial in order to prevent any attraction of arthropods by residual food. Each circle of traps was divided into three replicates of four traps each. Replicate A consisted of the first four traps in a clockwise direction from north, replicate B of the next four, etc.

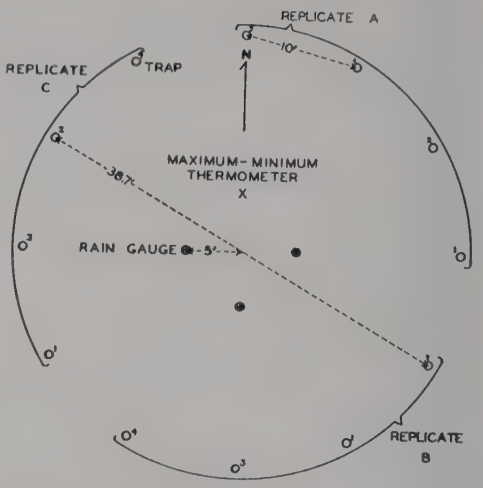

Fig. 2. Sample experimental setup of a trap circle. Numbers by traps refer to baits: 1-check; 2-cornmeal; 3-cantaloupe; 4-fish.

One trap in each replicate in each habitat (twelve traps in all) was left unbaited to serve as a check on the number and type of animals which entered the traps accidentally; likewise, one trap in each replicate was baited with 125 cc of fresh cornmeal, one was baited with a quarter of a ripe cantaloupe, and one with one-half pound of raw fish (carp). Within each replicate the arrangement of the baits was determined by drawing numbers.

The study was started June 24 and continued through August 6. Fresh baits, in clean cans, were put out when the old ones ceased to attract arthropods to any marked degree. The cornmeal traps were rebaited July 31; the cantaloupe traps were rebaited July 7 and July 27; the fish, July 13 and July 27. The amount of fish in these last two baitings was reduced to about a third of that of the first baiting, due to the tremendous numbers of insects attracted by the larger amount.

Every other day, usually in the afternoon, arthropods were collected from each trap. Forceps were the principal collecting device used. Forms which could readily fly escaped. Where possible, 100% collections were made of the remaining forms; however, certain of the smaller ones were sometimes so numerous that only a portion could be collected in the time available. Species too small to be noticed were frequently collected along with the debris adhering to the larger forms. All collections were preserved in vials of 70% alcohol and labeled as to date, habitat, bait, and replicate. The condition of the bait at the time of each collection was recorded. During

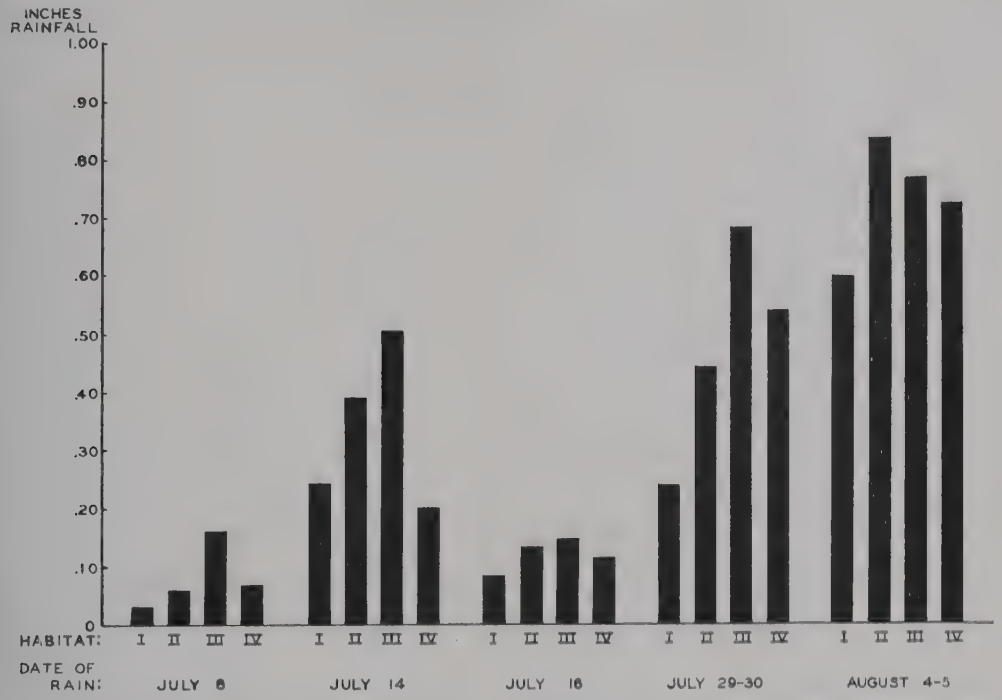

FIG. 3. Rainfall reaching the ground cover during period of study. The four habitats are I-mesic forest, II-bottom forest, III-ridge forest, IV-old field.

the course of the study 1008 collections were made.

MICROCLIMATIC CONDITIONS

It was possible to measure only a few of the microclimatic factors of the different habitats; however, these factors give an idea of other differences which must have occurred. The following factors were examined in this study: (1) rainfall at ground level, (2) maximum and minimum air temperatures at one foot above the substrate, (3) soil temperatures at a depth of about 4½ inches (11.5 cm). These factors were selected because they could be measured with the available equipment and in the available time because of their value as indicators of other factors.

Rainfall

In each of the four study areas were placed three simple rain gauges made of No. 10 cans with screen wire in the bottom to reduce splashing. The gauges were fixed on the surface of the ground and were located five feet east, south, and west of the center of each circle of traps (Fig. 2). No attempt was made to place the gauges in the open, so the "effective" rainfall rather than the total rainfall was measured. Water trickling down the trunks of trees was not measured. After each rain the rainfall was calculated from the volume of water collected in the gauges.

The relationships of the habitats as to amount of effective rainfall seem to have been rather variable, as the graphs in Figure 3 illustrate. In general, however, Habitats I, II, and III ranked in that order in terms of increasing effective rainfall. This is as would be expected, since these three habitats rank in the same order in terms of decreasing amount of vegetation which would intercept part of the rain, allowing it to evaporate without reaching the ground.

Although Habitat IV had the least intercepting vegetation (all the gauges in this habitat were completely in the open), the recorded rainfall in that habitat was in every case less than that of Habitat III and frequently less than that of Habitat II. The most reasonable explanation seems to be that the actual rainfall was less in this habitat than in the other three habitats. Two facts make this explanation plausible: (1) The rainfall was of the thundershower type in every instance. (2) The first three habitats are grouped rather closely and are all within 400 feet of an arm of Kentucky Lake known as Badger Creek, while Habitat IV is apart from the other study

areas and about one-third mile from Badger Creek (Fig. 1).

Other factors which might have contributed to the lack of correlation between readings in Habitat IV and those in the other three habitats are these: (1) The location of the gauges in Habitat III (and possibly Habitat II) might have been such that drainage from overhanging vegetation "funneled" an abnormal amount of rain into these gauges. This does not seem to be the case, since if the individual gauges are ranked in order of amount of rain caught during a particular rain, their order in relation to the habitat from which each comes is practically identical with the order of the totals from each habitat—*i.e.*, the amounts of rain caught by gauges in one habitat do not usually overlap with amounts caught by gauges in other habitats. In only one instance did a gauge in Habitat III have less water than did the gauge with the greatest catch in Habitat IV (2 cc less). Therefore, for this explanation to be correct, all three gauges in Habitat III would have to have been in spots of unusually high "effective" rainfall, and that seems unlikely. (2) Between time of rainfall and time of measurement, evaporation from the gauges in Habitat IV was probably greater than that in any of the other areas; however, in no case did more than part of a day elapse between rainfall and measurement, and amount of evaporation in Habitats IV and III should not have differed much, for the temperatures were quite similar. (3) A decrease in the catch of rain gauges may be due to the effect of wind eddying across their orifices. Since Habitat IV was the most open, wind effect should have been greatest in that habitat; however, the literature on wind effect, in general, points to differences of considerably less magnitude than those recorded in this study (Kittredge 1948).

The rainfall data from the study areas were compared with those from two nearby TVA rainfall stations—Johnsonville Steam Plant and Cavvia, located six and thirteen miles from the study areas (U. S. Dept. Commerce 1952). The spottiness of the rainfall during the course of the study is substantiated by the high variability in both dates of rainfall and amounts among the three localities (the two TVA stations and the study areas). In all three localities, however, rainfall until about the first of August was extremely light and infrequent. Indeed the whole area experienced the worst drought in many years as evidenced by the widespread browning of even mature trees on ridge sites and as confirmed by the local residents and by data compiled by TVA. Habitats III and IV were particularly affected by the drought conditions, in that a noticeable portion of the ground cover died during the course of the study.

Air Temperatures

In each of the four habitats a maximum-minimum thermometer of Six's type (gray plastic back, Taylor Instrument Company) was mounted horizontally on a ⅜ x 3 x 12 inch board facing north one foot above the substrate. Standard mountings held the thermometers about ½ inch from the mounting boards, permitting free circulation of air. In each habitat the installation was located five feet north of the center of the trap circle (Fig. 2). At each tending of the traps —*i.e.*, every other day from June 25 through August 6—the thermometers were read as to maxima and minima and reset. The thermometers were calibrated both before and after the study, and the readings were corrected accordingly.

An attempt was made to correlate U. S. Weather Bureau data with those from the study areas. The nearest station recording maximum and minimum temperatures was Paris, Tennessee, 27 miles NNW. The temperature data obtained at Paris showed the same trends as the data from the habitats (U. S. Dept. Commerce 1952).

Figure 4 shows graphically, for the period from June 25 through August 6, the absolute maximum temperature, the mean two-day maximum, the mean (obtained by averaging the mean maximum temperature with the mean minimum), the mean two-day minimum, and the absolute minimum for each of the study areas and for the USWB station at Paris. The data for Habitat II are partly derived by extrapolation, since it was discovered on July 9 that the thermometer had been stolen.

Although the extremes are slightly greater and the mean figures somewhat lower, the temperatures in Habitat I agree very closely with the USWB data. This agreement may be explained on the basis that the tight canopy and abundant understory produced a sheltered situation quite similar in effect to that of the slatted wooden box used by the USWB.

The absence of a well-developed shrub layer in Habitat II was probably responsible for the slightly greater extremes—both average and absolute—than those recorded in Habitat I. However, the sheltering effect of the vegetation in the case of maximum temperatures was still quite pronounced as compared to these effects in the remaining two habitats.

The data from Habitats III and IV show absolute maxima of about 122° F and mean maxima of about 111° F. These high readings were in

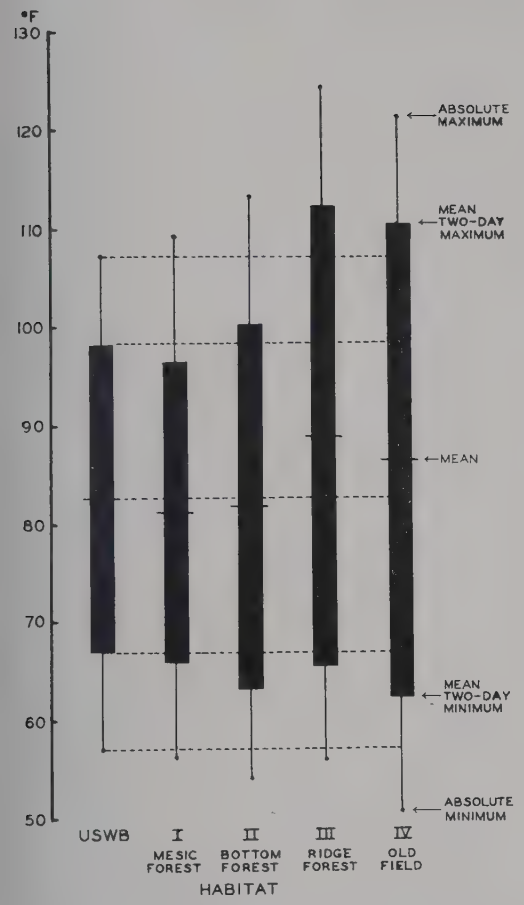

FIG. 4. Relationships of temperature in habitats, June 25 to August 6. Thermometers one foot above the ground. Data for Habitat II partly derived by extrapolation.

part due to heating by direct radiation, since both thermometers were almost completely in the open. Nevertheless, this effect was considrably lessened by the fact that the thermometers faced north. Although the maxima in Habitat III average higher than those in Habitat IV, the difference (1.8° F) may probably be ascribed to chance differences in heating by direct radiation, since Habitat III is in fact the more sheltered habitat. The minimum temperatures were consistently lowest in Habitat IV, where there was practically no tree or shrub cover which might retard heat loss at night.

Soil Temperatures

Soil temperatures in each habitat were taken with a glass laboratory thermometer every six days during the study. A rat-tail file was used to make a hole in the soil, and the thermometer was inserted to a depth of 4¾ inches. Readings were made to the nearest ½ degree Fahrenheit. Time of measurement varied from 10:30 a.m. to 5:30 p.m., but all measurements for any one day were made within narrower limits. Table I shows that Habitat IV had by far the highest diurnal soil temperatures, with recordings averaging 14.7° F above the mean for all four habitats and with a maximum of 103.5° F. The soil temperatures in Habitats I and II were about the same, with those in Habitat II being slightly higher in most cases. Soil temperatures in Habitat III averaged about 5° F higher than those in Habitats I and II.

TABLE I. Soil temperatures taken during period of study with a glass laboratory thermometer inserted to a depth of 4¾ inches

Date	Mean (°F)	Deviation from Mean				Range (°F)
		Habitat I	Habitat II	Habitat III	Habitat IV	
June 27	82.1	−6	−6.5	+3	+10	16.5
July 3	82.5	−7	−6.5	−2	+15.5	22.5
July 9	74.6	−4.5	−3.5	−3	+11.5	16
July 15	78.1	−6	−3.5	−3	+13	19
July 21	84.2	−8	−9	0	+17	26
July 27	83.1	−10	−5	−5	+20	30
Aug. 2	82.2	−9	−8	+1	+16	25
Average of all dates	81.0	−7.4	−6.1	−1.3	+14.7	22.1

Discussion

From the preceding microclimatic data, it is apparent that animals near, on, or in the ground in Habitats I and II were subjected to extremes of temperature much less than in the other two habitats. The remarkably high temperatures of both soil and air recorded in Habitat IV mark it as especially rigorous.

Although instruments to measure evaporation were not available, observations on soil moisture conditions and upon the process of decay of the baits indicated that Habitats I and II had almost equal evaporation rates, while Habitat III had a markedly higher rate and Habitat IV an even higher one. The differences in effective rainfall in the habitats did not compensate for differences in evaporation to any noticeable degree.

RESULTS OF COLLECTIONS

From Unbaited Traps

The three unbaited traps in each habitat served as checks on the numbers and kinds of animals which might be collected in a trap without direct relationship to the bait in that trap. In collecting from the unbaited traps, even very small specimens could be seen against the bare tin, so col-

lections were close to 100%. A total of 121 species of arthropods were collected from unbaited traps; Table II lists those species collected three or more times in at least one habitat.

TABLE II. Species collected three or more times from unbaited traps in at least one habitat. The first figure in each entry is the number of times the species was collected in check traps in that habitat; the second is the total number of specimens taken from check traps in that habitat

Species	Habitat			
	I	II	III	IV
Orthoptera				
Ceuthophilus stygius	3 - 3			
Ceuthophilus divergens		14 - 18		
Nemobius carolinus	.....	3 - 3*		
Coleoptera—Carabidae				
Carabus vinctus vinctus	.....	5 - 5		
Pasimachus depressus	.....	.....	4 - 4*	
Lepidoptera—Arctiidae				
Undetermined sp. (larvae)	.....	.....	.....	3 - 3*
Hymenoptera—Formicidae				
Stigmatomma p. pallipes	.....	.....	3 - 3*	
Aphaenogaster rudis	5 - 9			
Aphaenogaster treatae	.....	.....	3 - 3*	5 - 17**
Pheidole spp.				11 - 13
Crematogaster lineolata subopaca			11 - 19	20 - 44
Monomorium minimum	.....	.....	3 - 3*	
Myrmecina americana	3 - 3*			
Iridomyrmex pruinosus				13 - 22
Paratrechina parvula	11 - 12			5 - 10*
Phalangida				
Libitodes ornata	. . .	3 - 5		
Leiobunum nigripes	7 - 11	5 - 11*	.....	
Leiobunum politum	14 - 24	10 - 13		
Araneae				
Anahita punctulata	6 - 7			
Lycosa helluo		4 - 4*		
Pirata aluchua	16 - 20	5 - 6	.....	.....
Schizocosa crassipes		13 - 17	7 - 7	4 - 4*
Schizocosa retrorsa		9 - 10	.....	6 - 6
Latrodectus mactans				5 - 6

*Collected from only two of the three replicates in the habitat.
**Collected from only one of the three replicates in the habitat.

Since there was no attractant in the empty cans, the animals found in the check traps must have come upon them by chance. The actual entering of the traps, however, may have been due to a positive response to the conditions of temperature, moisture, and light associated with the trap. Certain arthropods that could easily escape, such as phalangids, nevertheless remained in the traps until the time of collection, possibly due to favorable conditions within the traps. On the other hand, arthropods such as ground beetles once in the trap could not escape.

The species collected from the check traps were mostly general predators or general scavengers which would be expected to move about more or less at random in the areas in which they occur. The species attracted in large numbers to the baited traps were seldom collected from the check traps, even though these were only a few yards away. For example, no carrion beetles (Silphidae) were found in check traps, whereas 1312 were collected from the traps baited with fish.

In general, species taken in check traps in a habitat were collected in all three replicates if they occurred with high enough frequency for this to be likely. In the case of the ant *Aphenogaster treatae* in Habitat IV, the location of a nest may have been responsible for its being collected five times from one check trap and never from the other two.

Differences among the habitats in the arthropods collected from the checks are striking. Indeed only one species was prominent in more than two habitats, and the majority were prominent only in one. Habitats I and II were characterized by an abundance of phalangids and spiders, while Habitats III and IV showed a predominance of ants. Habitat I showed a few ants, but Habitat II had none occurring with notable frequency. The camel cricket *Ceuthophilus divergens* was very prominent in Habitat II.

From Traps Baited with Cornmeal

Under the conditions of this study the cornmeal bait usually exhibited little decomposition, and there was little change in the arthropods collected from it. In a few instances the meal became sour and moldy as a result of rain water running into the can, and in such cases additional species were collected.

A total of 130 species were collected from cornmal traps. Table III lists for each habitat those species deemed attracted to the cornmeal. The following test was used as a criterion for attraction. For each species a null hypothesis was formulated that the probability of the species being taken was independent of whether the trap was baited or not. The probability of any resulting distribution of collections of a species from baited and unbaited traps could then be computed from the binomial $(p + q)^n$, where n is the number of collections and $p = q = \frac{1}{2}$. A probability value was obtained for each observed distribution which deviated, in favor of the baited traps, from that expected on the basis of the null hypothesis. Each value was the sum of the probabilities of equal and greater deviations in favor of the baited traps. Each was obtained from tables of the cumulative binomial distribution. If the probability was equal to or less than .05, the null hypothesis was rejected, and the species was considered to have been attracted to the bait.

At the risk of pointing out the obvious, species not included in the table may have been attracted

TABLE III. Species attracted to cornmeal-baited traps. See text for criterion used. The first figure in each entry is the number of times the species was collected in cornmeal traps in that habitat; the second is the total number of specimens taken from cornmeal traps in that habitat. The numbers in parentheses refer to the check-trap data for the same species

Species	Habitat			
	I	II	III	IV
Orthoptera				
Blattidae				
Parcoblatta uhleriana	8 - 17*	.	30 - 91	.....
Parcoblatta caudelli		.	20 - 37	6 - 8
Parcoblatta spp. (nymphs)	.....	.. .	26 - 50	.... .
Tettigoniidae				
Ceuthophilus stygius	15 - 22	.	7 - 9	.
	(3 - 3)	..	. .	. .
Ceuthophilus uhleri	13 - 20	.	9 - 14	. . .
Ceuthophilus divergens	14 - 24	29 - 65	7 - 9*	
	. .	(14 - 18)		.
Gryllidae				
Nemobius maculatus	6 - 9			.
Nemobius carolinus	10 - 12	11 - 17		..
	. .	(3 - 3)	.	
Nemobius confusus	8 - 10	.		...
Acheta assimilis	.	7 - 9*	7 - 8	
	.		(1 - 1)	
Hemiptera—Reduviidae				
Undetermined sp. (nymphs)	. . .		15 - 18	. .
	.		(1 - 1)	
Coleoptera				
Carabidae				
Platynus striatopunctatus	.	5 - 5	.	
Galerita bicolor	.	9 - 13	.	..
	.... .	(2 - 2)	.	. .
Chlaenius erythropus	.	5 - 5*		..
Nitidulidae				
Stelidota octomaculata	.	.	8 - 17*	..
Mycetophagidae				
Litargus didesmus	5 - 16*	8 - 23*		.. .
Hymenoptera—Formicidae				
Aphaenogaster rudis	20 - 36			..
	(5 - 9)	.....	.....	..
Aphaenogaster treatae			14 - 25	.. ...
	.		(3 - 3)	....
Monomorium minimum	....	.... .	10 - 89*	
	..	....	(3 - 3)	
Phalangida—Cosmetidae				
Libitiodes ornata	5 - 10*	.....	.....	.....

*Collected from only two of the three replicates in the habitat.

to the bait (and vice versa). For example, species collected less than five times cannot be included among the attracted, since at least five collections are necessary to produce probabilities small enough to reject the null hypothesis. Thus a species that was highly attracted, but rare, would not be listed.

The species considered, attracted to cornmeal may be divided into two groups. The first and largest group is composed of those species which occurred with more or less equal frequency throughout the period of study with little regard to the age and condition of the bait. All species listed in Table III, except *Stelidota octomaculata* and *Litargus didesmus,* belong in this category. There was considerable variation with the habitat as to which groups and species predominated (see Table III).

The second species group attracted to cornmeal in this study consists of only two species—the beetles *Stelidota octomaculata* and *Litargus didesmus.* These species were found only in cornmeal which had become moldy or sour. Since this occurred only in a few instances, the absence of the beetles in any particular habitat might have been due merely to a lack of an attractive bait.

A point of interest is that no insects which are considered pests of stored cornmeal (*e.g.,* mealworms, Indian-meal moth) were associated with any of the cornmeal baits during this study.

An important consideration in connection with the cornmeal baits is that except in the rare cases of wetting they remained identical in all habitats. Therefore, they should have had the same attractiveness in each habitat, and the differences in the species attracted should have been due to differences in the species within and about the habitat. The fact that no species was attracted in all four habitats and only one was attracted in three of the habitats seems to indicate that no forms came from great distances. Whatever attractiveness the cornmeal had must have been of short range.

Table IV, derived from the data in Table III, is a summary of the similarities among the four habitats as to the species attracted to cornmeal.

TABLE IV. Similarities in the species attracted to cornmeal in the four habitats

Habitat	Total spp. attracted to cornmeal	% OF SPECIES ALSO ATTRACTED IN HABITAT			
		I	II	III	IV
I	10	..	30	40	0
II	7	43	..	29	0
III	10	40	20	..	10
IV	1	0	0	100	

The wooded habitats—I, II, and III—all have species in common, whereas the lone species attracted in Habitat IV is shared only by Habitat III, the driest of the other three.

From Traps Baited with Cantaloupe

Some 278 species were collected from the cantaloupe baits. Table V lists for each habitat those species attracted to the cantaloupe. The same statistical test was used as a criterion of attraction as in the case of the collections from cornmeal. The application of the test to the cantaloupe collections has this weakness: The collection of freely flying forms depended upon their becoming entrapped in the liquid associated with decomposition. Hence for these forms, the check trap data have no real

TABLE V. Species attracted to cantaloupe-baited traps. The first figure in each entry is the number of times the species was collected in cantaloupe traps in that habitat; the second is the total number of specimens taken from cantaloupe traps in that habitat. The numbers in parentheses refer to the check-trap data for the same species

Species	Habitat I	Habitat II	Habitat III	Habitat IV
Diplopoda				
Narceus americanus	.....	.....	5 - 5	.....
Orthoptera				
Blattidae				
Ischnoptera deropeltiformis	.....	6 - 7*	5 - 5*	.....
Parcoblatta uhleriana	13 - 22	.....	20 - 97	.....
Parcoblatta caudelli	.....	.....	17 - 31	14 - 48
Parcoblatta spp. (nymphs)	9 - 32	.....	28 - 115	7 - 8*
Tettigoniidae				
Ceuthophilus stygius	.....	9 - 15*	.....	.....
	.....	(1 - 1)	.....	.....
Ceuthophilus uhleri	.....	.....	5 - 8	.....
Coleoptera				
Carabidae				
Evarthrus americanus	6 - 6	.....	.....	.....
Platynus tenuis	7 - 25**	.....	.....	.....
Hydrophilidae				
Cercyon analis	38 - 151	33 - 114	.....	.....
Leiodidae				
Colenis impunctata	.....	.....	5 - 5*	.....
Staphylinidae				
Oxytelus sp.	39 - 170	52 - 295	41 - 224	.....
	.....	(1 - 1)	.....	.....
Aderocharis corticinus	7 - 8	5 - 6*	.....	.....
Rugilus sp.	6 - 8*	13 - 19	.....	.....
Philonthus cyanipennis	.....	6 - 7*	.....	.....
Philonthus blandus	13 - 28	9 - 13	.....	.....
Philonthus sp. #1	11 - 14	10 - 16	11 - 21	.....
Philonthus sp. #2	.....	7 - 8	.....	.....
Belonuchus formosus	11 - 22	18 - 35	8 - 11	.....
Platydracus sp. #1 and *maculosus*	5 - 5	16 - 24	.....	.....
Platydracus fossator	18 - 24	7 - 9*	18 - 23	.....
	(2 - 2)	.....	.....	.....
Tachinus fimbriatus	6 - 13	6 - 7*	.....	.....
Tachinus pallipes	.....	5 - 7*	.....	.....
Lordithon azillaris	5 - 7*	.....	.....	.....
Atheta spp.	29 - 61	29 - 65	31 62	.....
Ptiliidae				
Sp. #1	5 - 5	.....	.....	.....
Histeridae				
Hister abbreviatus	.....	5 - 7*	.....	.....
Hister depurator	.....	8 - 11	5 - 5	.....
Phelister mobilensis	5 - 5	.....	16 - 21	.....
Nitidulidae				
Carpophilus sayi	.....	.....	14 - 62	10 - 85
Stelidota geminata	24 - 179	20 - 53	19 - 50	.....
Stelidota octomaculata	.....	.....	5 - 5	.....
Pallodes pallidus	.....	.....	6 - 6	.....
Glischrochilus obtusus	5 - 5*	.....	.....	.....
Glischrochilus fasciatus	.....	.....	7 - 10	.....
Glischrochilus q. quadrisignatus	6 - 9	10 - 22	10 - 17	.....
Mycetophagidae				
Typhaea stercorea	.....	.....	.....	9 - 84
Scarabaeidae				
Deltochilum gibbosum	5 - 7	15 - 42	.....	.....
Ateuchus histeroides	.....	7 - 13	8 - 16*	.....
Onthophagus hecate	18 - 31	63 - 490	6 - 7	.....
	.....	(1 - 1)	.....	.....
Onthophagus striatulus	.....	8 - 13	5 - 5*	.....
	.....	(1 - 1)	.....	.....
Onthophagus pennsylvanicus	8 - 9	13 - 20	.....	.....
Ataenius platensis	.....	.....	.....	9 - 20
Geotrupes splendidus	10 - 15	17 - 36	7 - 9	.....

TABLE V. Continued

Species	Habitat I	Habitat II	Habitat III	Habitat IV
Diptera				
Stratiomyidae				
Undetermined spp. (larvae)	25 - 97	30 - 86	16 - 52	.....
Drosophilidae				
Undetermined spp. (larvae)	8 - 17	16 - 42	7 - 11	.....
Sphaeroceridae				
Leptocera winnemana	8 - 8	20 - 42	.....	.....
Sphaerocera annulicornis	12 - 12	6 - 8	.....	.....
Sarcophagidae				
Undetermined spp. (larvae)	.....	14 - 33	7 - 34	9 - 23
	.....	(1 - 1)	.....	.....
Hymenoptera				
Pteromalidae				
Spalangia sp.	.....	5 - 5*	.....	.....
Formicidae				
Crematogaster lineolata subopaca	.....	.....	.....	35 - 139
	.....	.....	.....	(20 - 44)
Irudomyrmex pruinosus	.....	.....	.....	28 - 68
	.....	.....	.....	(13 - 22)
Camponotus pennsylvanicus	12 - 79	14 - 20	.....	.....
	.....	(2 - 2)	.....	.....
Prenolepis imparis	9 - 46*	.....	.....	.....
Araneae—Salticidae				
Sitticus cursor	.....	.....	.....	5 - 5
Acarina				
Undetermined spp.	14 - 99	49 - 358	17 - 76	.....
	(2 - 2)	(1 - 1)	(3 - 3)	.....

*Collected from only two of the three replicates in the habitat.
**Collected from only one of the three replicates in the habitat.

meaning and there can be no good test of attraction. However, three of these forms are included in the table on the basis that species which could not escape are usually classed as attracted when collected in similar numbers.

There are three other important limitations to the data recorded in Table V: (1) The fact that no adult flies were collected in large numbers from cantaloupe in Habitats III and IV almost certainly resulted from a lack of ensnaring liquid rather than an absence of flies. The scarcity of collections of adults of those species common as larvae confirms this judgment. (2) In the case of species less than 5 mm in length, the number of individuals has little significance since they were sometimes so abundant that collection of all the individuals was impossible in the time available. An attempt was made to collect a sample large enough to insure the inclusion of all important species. (3) In a few taxonomic groups, such as the mites, species were not separated. Such groups must be included in the table because of their prominence in the collections, even though it is misleading to compare directly data for groups of species with those for single species.

The cantaloupe bait differed from the cornmeal in that it had a definite course of decay in each habitat. As the cantaloupe decomposed, there

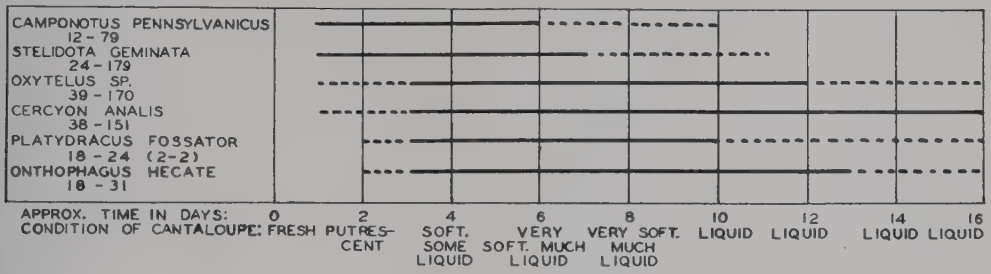
CAMPONOTUS PENNSYLVANICUS
12 - 79
STELIDOTA GEMINATA
24 - 179
OXYTELUS SP.
39 - 170
CERCYON ANALIS
38 - 151
PLATYDRACUS FOSSATOR
18 - 24 (2-2)
ONTHOPHAGUS HECATE
18 - 31
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF CANTALOUPE: FRESH PUTRES-CENT SOFT. SOME LIQUID VERY SOFT. MUCH LIQUID VERY SOFT. MUCH LIQUID LIQUID LIQUID LIQUID

FIG. 5. Changes in attractiveness of cantaloupe in Habitat I (mesic forest). The number of times the species was collected and the total number of individuals collected are indicated below each species name. Figures in parentheses refer to check-trap data for the same species. The line after each species name refers to the presence of the species at various stages of decay. The relative abundance of a given species at different times is indicated by a solid line (abundant) or a broken line (scarce).

were marked changes in the numbers and species of arthropods attracted to it. The course of decay varied a great deal from habitat to habitat. The most important factor was probably the rate of evaporation from the traps. The variations recorded in soil and air temperatures (Table I and Fig. 4) give some indication of the differing conditions under which the baits in different habitats decayed. In Habitats I and II the cantaloupe became soft and mushy and finally decomposed into a watery liquid. In Habitat III the initial stages were similar to those in the preceding habitats, but instead of finally becoming a watery liquid the mush dried to a hard cake-like substance. In Habitat IV drying was evident from the first, the final product being the shriveled, dried remains of the original section of cantaloupe.

Figure 5 shows graphically the changes in attractiveness of the cantaloupe baits in Habitat I to the most important species associated with them. Species included are those which occurred in three or more of the nine sequences (three baitings, each with three replicates) studied *and* which either were collected in numbers of at least thirty or were collected at least fifteen times in excess of check-trap data. These arbitrary limits correspond roughly to the minimum data required to judge a species as to the relative attractiveness of cantaloupe in various stages of decomposition. Groups which could not be separated to species—e.g. *Atheta* spp.—are not included, since individual species within such groups do not necessarily have similar responses to the bait. The horizontal scale of the graph indicates the stage of decomposition of the cantaloupe. Condition of the bait is described at regular intervals, each interval representing approximately two days. The exact time intervals occupied by the various stages of decay varied somewhat among the three baitings and among the three replicates. The presence of a species at any particular stage of decay is shown by a line (either solid or broken). Figures 6, 7, and 8 show the same information for Habitats II, III, and IV respectively.

Table 5 and Figures 5 to 8 show important differences in the species attracted to the cantaloupe baits in the four habitats. These differences resulted from two factors: (1) differences in the arthropods in the vicinities of the habitats and (2) differences in the baits in the habitats (due

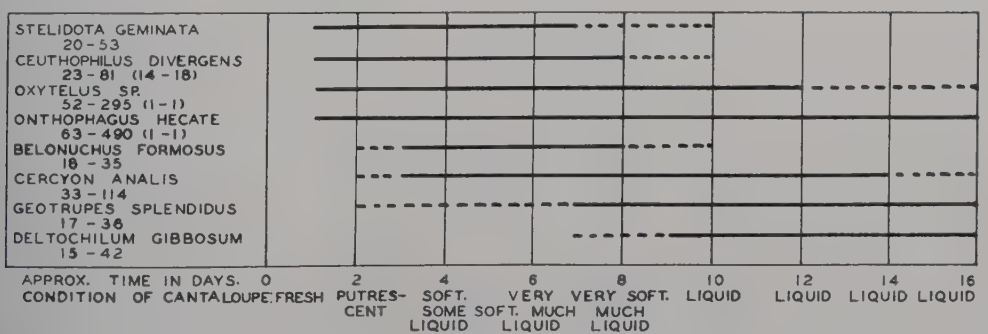
STELIDOTA GEMINATA
20 - 53
CEUTHOPHILUS DIVERGENS
23 - 81 (14 - 18)
OXYTELUS SP.
52 - 295 (1 - 1)
ONTHOPHAGUS HECATE
63 - 490 (1 - 1)
BELONUCHUS FORMOSUS
18 - 35
CERCYON ANALIS
33 - 114
GEOTRUPES SPLENDIDUS
17 - 36
DELTOCHILUM GIBBOSUM
15 - 42
APPROX. TIME IN DAYS. 0 2 4 6 8 10 12 14 16
CONDITION OF CANTALOUPE: FRESH PUTRES-CENT SOFT. SOME LIQUID VERY SOFT. MUCH LIQUID VERY SOFT. MUCH LIQUID LIQUID LIQUID LIQUID

FIG. 6. Changes in attractiveness of cantaloupe in Habitat II (bottom forest). See Fig. 5 for explanation.

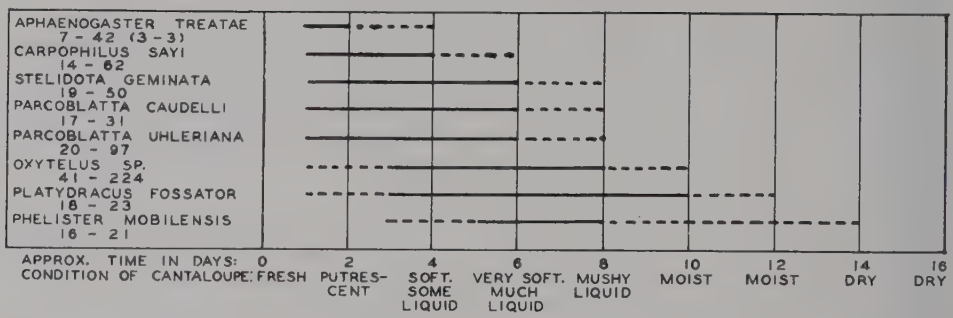
APHAENOGASTER TREATAE
7 - 42 (3 - 3)
CARPOPHILUS SAYI
14 - 62
STELIDOTA GEMINATA
19 - 50
PARCOBLATTA CAUDELLI
17 - 31
PARCOBLATTA UHLERIANA
20 - 97
OXYTELUS SP.
41 - 224
PLATYDRACUS FOSSATOR
18 - 23
PHELISTER MOBILENSIS
16 - 21
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF CANTALOUPE: FRESH PUTRES-CENT SOFT. SOME LIQUID VERY SOFT. MUCH LIQUID MUSHY LIQUID MOIST MOIST DRY DRY

FIG. 7. Changes in attractiveness of cantaloupe in Habitat III (ridge forest). See Fig. 5 for explanation.

to differences in the course of decay). In the case of the check traps and the dry cornmeal traps, only the first factor was operative.

TABLE VI. Similarities in the species attracted to cantaloupe in the four habitats

Habitat	Total spp. attracted to cantaloupe	% OF SPECIES ALSO ATTRACTED IN HABITAT			
		I	II	III	IV
I	26	..	69	38	0
II	28	64	..	43	0
III	22	45	55	..	9
IV	7	0	0	29	..

Table VI, derived from the data in Table V, is a summary of the similarities among the four habitats as to the species collected at cantaloupe. Only separate species were included in the tabulation—*i.e.* groups not determined to species were omitted. Habitats I and II are shown to be more closely related in their cantaloupe fauna than any other two habitats. Habitat III is related almost equally to Habitats I and II and has two species in common with Habitat IV. Five of the seven important species on cantaloupe in Habitat IV are of importance only in that habitat.

From Traps Baited with Fish

There were 255 species collected from fish-baited traps. Table VII lists for each habitat those species attracted to the fish. The same criterion of attraction as before was used, and the same limitations apply to these data as applied in the case of the cantaloupe data.

Like the cantaloupe baits, the fish baits decomposed somewhat differently in the various habitats. Again the most important factor was probably the rate of evaporation from the traps. In Habitats I and II the fish became putrid and soft until finally it was reduced to a foul-smelling liquid. This liquid gradually dried until a mild-smelling solid remained. In Habitat III the fish became putrid and soft but soon began to dry, and the pieces were more or less intact at the end of the process. In Habitat IV drying began immediately, and the portions of fish soon became hard and leathery.

Figures 9 to 12 show the changes in attractiveness of the fish baits in the four habitats. The data are presented in the same manner as in the preceding four figures.

Table VIII was compiled from the data in Table VII and summarizes the similarities in the species collected at fish in the four habitats. These similarities fall into much the same pattern as they did in the cantaloupe bait. The presence in Habitats I and II of small percentages of the species important in Habitat IV is the only major difference.

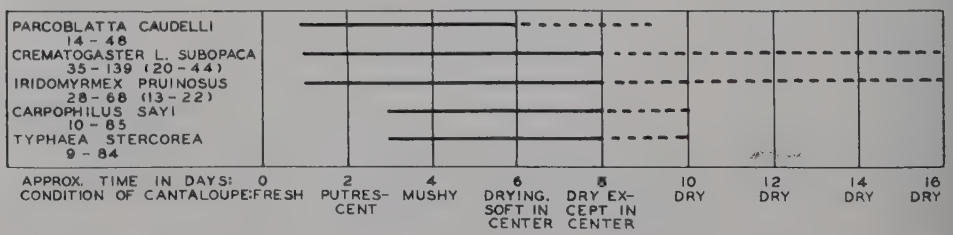
PARCOBLATTA CAUDELLI
14 - 46
CREMATOGASTER L. SUBOPACA
35 - 139 (20 - 44)
IRIDOMYRMEX PRUINOSUS
28 - 68 (13 - 22)
CARPOPHILUS SAYI
10 - 85
TYPHAEA STERCOREA
9 - 84
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF CANTALOUPE: FRESH PUTRES-CENT MUSHY DRYING. SOFT IN CENTER DRY EX-CEPT IN CENTER DRY DRY DRY DRY

FIG. 8. Changes in attractiveness of cantaloupe in Habitat IV (old field). See Fig. 5 for explanation.

TABLE VII. Species attracted to fish-baited traps. The first figure in each entry is the number of times the species was collected in fish traps in that habitat; the second is the total number of specimens taken from fish traps in that habitat. The numbers in parentheses refer to the check-trap data for the same species

Species	Habitat I	Habitat II	Habitat III	Habitat IV
Diplopoda				
Narceus americanus			10 - 11	
Orthoptera				
Blattidae				
Parcoblatta uhleriana	.....	.....	18 - 48	.....
Parcoblatta caudelli	.....	.....	10 - 16*	7 - 12
Parcoblatta spp. (nymphs)	.....	.....	10 - 18	.....
Tettigoniidae				
Ceuthophilus divergens	.....	.....	5 - 8	.....
Hemiptera—Coriscidae				
Coriscus eurinus	.....	.....	.....	17 - 31
Coleoptera				
Carabidae				
Chlaenius erythropus	5 - 5	.....	.....	
Hydrophilidae				
Cercyon analis	15 - 21	.....	.....	.....
Pemelus costatus	10 - 12	.....	.....	.....
Silphidae				
Nicrophorus orbicollis	36 - 153	25 - 175	21 - 70	6 - 7
Nicrophorus americanus	.....	9 - 9	.....	.....
Nicrophorus pustulatus	.....	.....	5 - 13*	.....
Nicrophorus tomentosus	15 - 21	9 - 19*	6 - 11*	.....
Silpha littoralis surinamensis	19 - 268	6 - 22*	17 - 253	.....
Silpha lit. surinamensis (larvae)	6 - 27*	.....	.....	.....
Thanatophilus americana	24 - 91	18 - 42	14 - 29	.....
Nemadus horni	5 - 6*	.....	.....	.....
Prionochaeta opaca	23 - 62	13 - 18	.....	.....
Staphylinidae				
Oxytelus insignitus		10 - 61	.....	
Oxytelus sp.	36 - 463	27 - 298	31 - 285	5 - 8*
	.....	(1 - 1)	.....	.....
Rugilus sp.	8 - 8	14 - 31	.....	.....
Philonthus cyanipennis	5 - 5*	.....	.....	.....
Philonthus sp. #1	9 - 12	.....	6 - 7	.....
Philonthus sp. #2	5 - 5	.....	.....	.....
Philonthus sp. #3	.....	5 - 7**	.....	.....
Philonthus sp. #4	6 - 6	.....	.....	.....
Platydracus maculosus	15 - 27	24 - 56	5 - 6	.....
Platydracus sp. #1	18 - 26	14 - 31	30 - 57	9 - 15
Platydracus femoratus	7 - 7	9 - 26	.....	.....
Platydracus fossator	31 - 41	10 - 11	16 - 17	.....
	(2 - 2)	.....	.....	.....
Ontholestes cingulatus	10 - 12	21 - 40	.....	.....
Staphylinus maxillosus	.....	.....	15 - 34	5 - 7
Tachinus pallipes	.....	6 - 8	.....	.....
Atheta spp.	22 - 34	21 - 87	10 - 16	.....
Aleochara sp.	24 - 44	17 - 58	8 - 11	.....
Baryodma sp.	.....	.....	.....	5 - 6
Ptiliidae				
Sp. #1	5 - 10*			
Histeridae				
Hister coenosus	14 - 24	14 - 24	14 - 23	.....
Hister abbreviatus	16 - 30	21 - 36	9 - 23	.....
Hister depurator	23 - 44	23 - 62	12- 19	
Atholus sedecimstriatus		5 - 7*		.....
Phelister mobilensis	.....	6 - 6	15 - 22	.....
Saprinus assimilis	47 - 240	33 - 281	46 - 438	13 - 21
Saprinus semistriatus	.....	.....	13 - 19	5 - 8
Saprinus orbiculatus	.....	.....	.....	10 - 35
Dermestidae				
Dermestes caninus			21 - 55	33 - 184
Undetermined spp. (larvae)	.....	.....	.....	7 - 21
Nitidulidae				
Omosita colon	6 - 7*	8 - 17*	13 - 23	5 - 7

TABLE VII. Continued

Species	Habitat I	Habitat II	Habitat III	Habitat IV
Monotomidae				
Monotoma americana	.....	.....	.....	5 - 15*
Scarabaeidae				
Deltochilum gibbosum	20 - 31	19 - 49	16 - 30	
Ateuchus histeroides	7 - 12	.....	8 - 12	.....
Onthophagus hecate	6 - 6	19 - 46	6 - 6	....
	.....	(1 - 1)	.....	....
Onthophagus pennsylvanicus		6 - 12*	13 - 21	
Ataenius platensis	.....	.....	.....	13 - 31
Geotrupes splendidus	14 - 24	18 - 33	16 - 22	.....
Trogidae				
Troz monachus	13 - 21	13 - 18	9 - 10	.....
Troz asper	.....	.....	.....	15 - 23
Diptera				
Empididae				
Drapetis sp.	.....	9 - 20	12 - 19	
Phoridae				
Conicera atra	7 - 8	.....	....	
Diploneura cornuta	13 - 83	11 - 196*	6 - 22	.....
Diploneura incisuralis	.....	6 - 41*	.....	.....
Megaselia scalaris	.....	8 - 28*	.....	....
Megaselia juli	7 - 8	7 - 29*	.....	
Megaselia spp.	10 - 13	13 - 37*	.....	.....
Puliciphora sp. (wingless ♀ ♀)	18 - 43	7 - 27	14 - 19	....
Drosophilidae				
Undetermined spp. (larvae)	.....	6 - 12	.....	
Chloropidae				
Hippelates bishoppi	.....	6 - 18*	.....	
Sphaeroceridae				
Leptocera fontinalis	13 - 49	8 - 29	.....	.....
Leptocera winnemana	19 - 60	9 - 26	5 - 7	
Leptocera undescribed sp.	9 - 26	.....	.....	.....
Leptocera sp. #1	23 - 127	15 - 70	7 - 12*	
Leptocera sp. #2	15 - 44	8 - 19*	.....	.....
Leptocera sp. #3	8 - 10	.....	.....	.....
Leptocera sp. #4	7 - 18			
Sphaerocera annulicornis	10 - 14	9 - 11	.....	.....
Sphaerocera undescribed sp.	7 - 12	11 - 31*		
Muscidae				
Fannia sp. (larvae)	9 - 17*	9 - 18	.....	
Sarcophagidae				
Sarcophaga bullata	5 - 10	.....	.....	.....
Undetermined spp. (larvae)	47 - 305	22 - 114	54 - 287	39 - 258
	.....	(1 - 1)	...	..
Calliphoridae				
Phormia regina	6 - 14	.....	.....	.....
Undetermined spp. (larvae)	.....	5 - 37*	.....	6 - 7
Hymenoptera—Formicidae				
Crematogaster lineolata subopaca	.....	.....	.....	29 - 120
	.....	.....	.....	(20 - 44)
Camponotus pennsylvanicus	6 - 7*	.....	.....	....
Paratrechina parvula	.....	.....	.....	10 - 15
	.....	.....	.....	(5 - 10)
Araneae—Thomisidae				
Xysticus ferox			14 - 20	
Acarina				
Undetermined spp.	52- 563	31 - 516	28 - 304	10 - 56
	(2 - 2)	(1 - 1)	(3 - 3)	

*Collected from only two of the three replicates in the habitat.
**Collected from only one of the three replicates in the habitat.

DISCUSSION

When the total collections of arthropods from all traps in all habitats are considered, the same relationships among habitats are exhibited as in the more limited cases of the species classed as

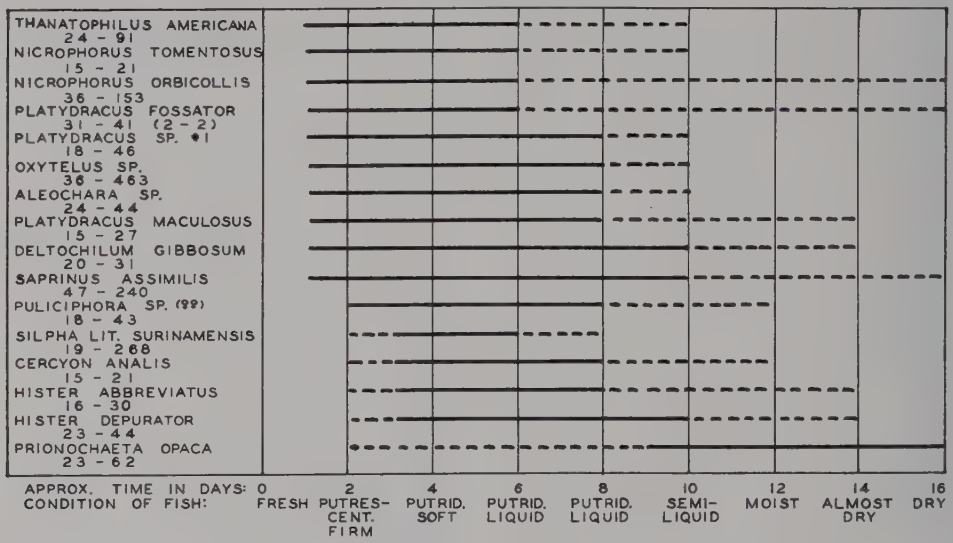
THANATOPHILUS AMERICANA 24 - 91
NICROPHORUS TOMENTOSUS 15 - 21
NICROPHORUS ORBICOLLIS 36 - 153
PLATYDRACUS FOSSATOR 31 - 41 (2 - 2)
PLATYDRACUS SP. #1 18 - 46
OXYTELUS SP. 36 - 463
ALEOCHARA SP. 24 - 44
PLATYDRACUS MACULOSUS 15 - 27
DELTOCHILUM GIBBOSUM 20 - 31
SAPRINUS ASSIMILIS 47 - 240
PULICIPHORA SP. (??) 18 - 43
SILPHA LIT. SURINAMENSIS 19 - 268
CERCYON ANALIS 15 - 21
HISTER ABBREVIATUS 16 - 30
HISTER DEPURATOR 23 - 44
PRIONOCHAETA OPACA 23 - 62
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF FISH: FRESH PUTRES-CENT. FIRM PUTRID. SOFT PUTRID. LIQUID PUTRID. LIQUID SEMI-LIQUID MOIST ALMOST DRY DRY

FIG. 9. Changes in attractiveness of fish in Habitat I (mesic forest). See Fig. 5 for explanation.

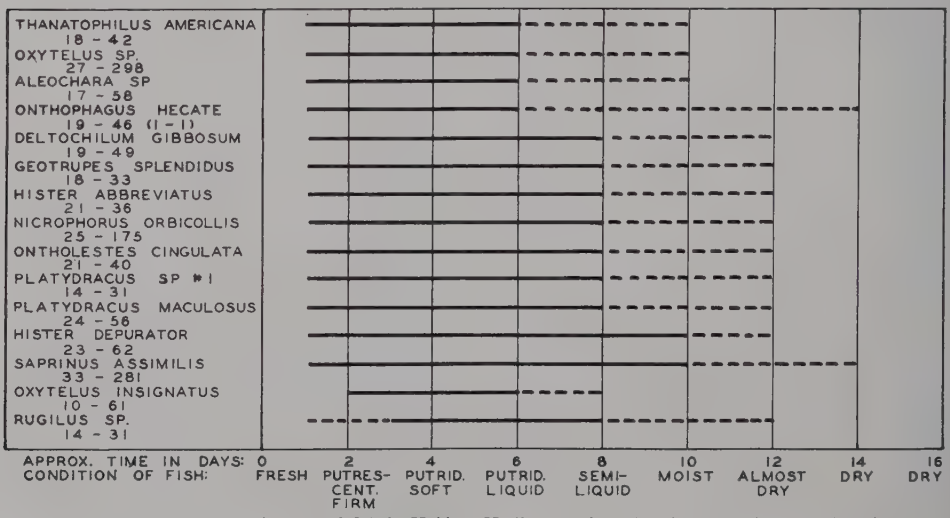
THANATOPHILUS AMERICANA 18 - 42
OXYTELUS SP. 27 - 298
ALEOCHARA SP 17 - 58
ONTHOPHAGUS HECATE 19 - 46 (1 - 1)
DELTOCHILUM GIBBOSUM 19 - 49
GEOTRUPES SPLENDIDUS 18 - 33
HISTER ABBREVIATUS 21 - 36
NICROPHORUS ORBICOLLIS 25 - 175
ONTHOLESTES CINGULATA 21 - 40
PLATYDRACUS SP #1 14 - 31
PLATYDRACUS MACULOSUS 24 - 56
HISTER DEPURATOR 23 - 62
SAPRINUS ASSIMILIS 33 - 281
OXYTELUS INSIGNATUS 10 - 61
RUGILUS SP. 14 - 31
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF FISH: FRESH PUTRES-CENT. FIRM PUTRID. SOFT PUTRID. LIQUID SEMI-LIQUID MOIST ALMOST DRY DRY DRY

FIG. 10. Changes in attractiveness of fish in Habitat II (bottom forest). See Fig. 5 for explanation.

attracted to individual baits. Table IX is a summary of the similarities among habitats on the basis of all collections. Habitats I and II are clearly more alike than any other two habitats in respect to the species collected. Habitat III is nearly equally related to these two. Habitat IV has no close similarities with any of the other three habitats but is closest to Habit III, the driest of the wooded habitats. These relationships correlate nicely with the vegetational and microclimatic relationships recorded.

The degree of difference among the collections in the four habitats is shown by the fact that out of a total of 444 species of arthropods, 224 were collected in only one habitat, 107 were collected in two habitats, 81 in three habitats, and only 32 in all four habitats.

SUMMARY

Four habitats of differing vegetation in Benton County, Tennessee, were studied in the summer of 1952 to determine what sorts of similarities

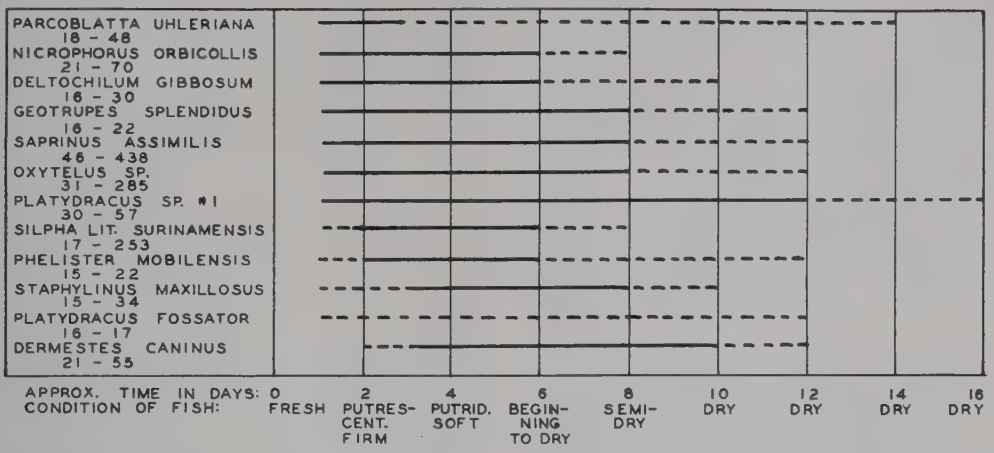

FIG. 11. Changes in attractiveness of fish in Habitat III (ridge forest). See Fig. 5 for explanation.

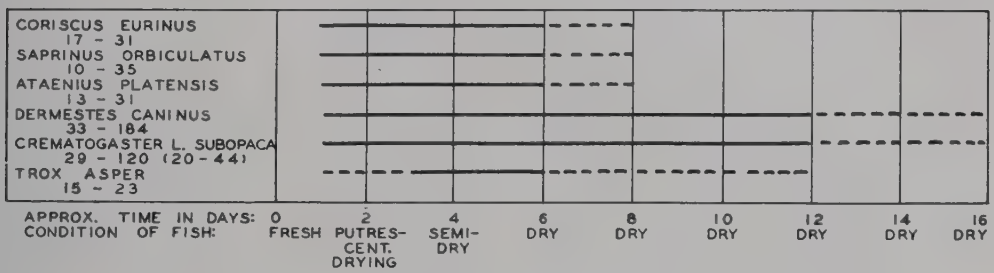
CORISCUS EURINUS
17 - 31
SAPRINUS ORBICULATUS
10 - 35
ATAENIUS PLATENSIS
13 - 31
DERMESTES CANINUS
33 - 184
CREMATOGASTER L. SUBOPACA
29 - 120 (20 - 44)
TROX ASPER
15 - 23
APPROX. TIME IN DAYS: 0 2 4 6 8 10 12 14 16
CONDITION OF FISH: FRESH PUTRES-CENT. DRYING SEMI-DRY DRY DRY DRY DRY DRY DRY

FIG. 12. Changes in attractiveness of fish in Habitat IV (old field). See Fig. 5 for explanation.

TABLE VIII. Similarities in the species attracted to fish in the four habitats

Habitat	Total spp. attracted to fish	% of Species also Attracted in Habitat			
		I	II	III	IV
I	50	..	66	48	10
II	43	77	..	56	12
III	35	69	69	..	26
IV	17	29	29	53	..

TABLE IX. Similarities in the species collected in the four habitats. A total of 444 species are considered

Habitat	Total spp. collected in Habitat	% of Species also Collected in Habitat			
		I	II	III	IV
I	230	..	67	54	20
II	248	62	..	47	19
III	213	58	55	..	26
IV	118	39	39	47	..

and differences may occur in the arthropods associated with decaying materials in different habitats in the same area.

Habitat I was in a mesic valley dominated by a maple-gum-oak forest. Habitat II was in a creek bottom with a park-like stand of large oak, gum, hickory, and tulip trees. Habitat III was a dry ridge which had a broken-canopied stand of oak. Habitat IV was on a south-facing slope in a rocky abandoned field.

A study of the microclimates of the habitats showed that the habitats ranked I, II, III in order of increasing effective rainfall. Habitat IV was variable in its relationship with the other habitats but always showed less rainfall than Habitat III. Air temperature extremes at the one-foot level in Habitats III and IV were much greater than in Habitats I and II. Midday soil temperatures at 4½ inches in Habitat IV averaged 15° F higher than similar temperatures in Habitat III and over 20° F higher than those in Habitats I and II. Observations on the drying of soils and baits indicated that evaporation was greatest in Habitat IV and least in Habitats I and II.

In each habitat ground traps replicated three times were used to study the arthropods associated with cornmeal, cantaloupe, and fish. Unbaited traps were used to determine what ani-

mals entered the traps without regard to the bait.

Arthropods collected in unbaited traps were general predators or scavengers. Species attracted in large numbers to baited traps were seldom collected from near-by check traps. The species and higher groups taken in unbaited traps varied widely among the habitats.

Except in cases of wetting, the cornmeal baits underwent little change. Nevertheless, 17 species were shown to be attracted to the unaltered meal. The species present suggest that none was attracted from outside the immediate vicinity of the traps.

Cantaloupe underwent a definite course of decay which varied with the habitat. The species associated with cantaloupe changed in kind and number as decomposition progressed. Forty-eight species were shown to be attracted to cantaloupe.

Fish was like cantaloupe in that it underwent a definite course of decay in each habitat and that the associated species changed in kind and number as decomposition progressed. Seventy-seven species were shown to be attracted to fish.

A comparison of the species of arthropods shown to be attracted to fish and cantaloupe in each habitat with those shown to be attracted to the same materials in the other habitats shows that Habitats I and II had more species in common than any other two habitats. Similarly Habitat III was more closely related to I and II than to IV, but had more species in common with IV than did I and II. Of the four habitats, Habitat IV had fewest species and the smallest percentages of these in common with other habitats. When all 444 species collected during the study are considered, the relationships among the habitats, as to species collected in more than one habitat, are the same as above. These relationships are correlated with the observed relationships of the courses of decay in the habitats, and these latter relationships in turn depend largely on the microclimates of the habitats.

The degree of difference in the collections from the various habitats is illustrated by the fact that of the 444 species collected, only 32 species were collected in all four habitats, and 224 species were collected in only one of the four habitats.

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MICROCLIMATIC PATTERNS IN THE ARMY ANT BIVOUAC

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Introduction

The army ants of the New World of the subgenus *Eciton* are characterized by a nomadic pattern of life, the establishment of bivouacs or temporary nests in relatively exposed, generally non-subterranean sites, and a carnivorous diet. The study of the bivouac formation and structure as influenced by the microclimate provides a basis for considering the adaptive significance of this behavior pattern.

Previous investigations had indicated the relative stability of intrabivouac thermal patterns and the reduced range of temperature and relative humidity fluctuations at the bivouac site (Schneirla, Brown, and Brown 1954). The purpose of this investigation was to continue and expand investigations on microclimatic patterns in relation to bivouac formation and structure.

The bivouac of *Eciton hæmatum* Fabricius,

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formed wholly by the ants' own bodies clustered together, generally hangs from an overheard support such as a fallen branch or log to the ground. Typically, it takes the approximate form of a cyclinder but is frequently modified by environmental variations. Bivouacs vary up to about 25 cm in height and 50 cm in diameter.

The colony passes through two distinct, regular, and alternating behavioral phases that influence the location and formation of the bivouac. The nomadic phase in *E. hamatum,* usually lasting 16-17 days, is characterized by large, daily raids terminating late in each day with the emigration of the entire colony and the formation of a new bivouac. The statary phase, which follows and usually lasts 20 days, is characterized by a single bivouac site, no daily emigrations, and sporadic daily raids.

The basis for this precise rhythm is the cumulative excitatory effect of the brood or broods within the bivouac. Briefly, the statary phase commences when the mature larvae spin cocoons and reduce the excitatory level (both chemical and tactual) of the colony. Eggs are laid midway in this phase, but not until the callow adults appear is the excitatory level raised sufficiently to initiate the nomadic phase. Thus started, it is maintained by the developing larvae. A much more detailed review of the development of these concepts may be found in Schneirla *et al.* (1954). Terms used in this paper for colony designations, bivouac types and locations, and behavioral phases are those adopted by Schneirla (1949) and Schneirla *et al.* (1954).

The present study, carried out on Barro Colorado Island in the Panama Canal Zone, was initiated early in the dry season (January) of 1952 and extended into the initial portion of the wet season (May). This island, roughly 3 by 2.5 miles, is covered almost entirely by mature, seasonal evergreen forest, although scattered patches cut over in past years are now occupied by somewhat younger successional stages (Richards 1952).

The main expenses of this project were sustained through grant number 72, awarded by the American Philosophical Society. The investigation was arranged through the cooperation of Dr. T. C. Schneirla, in connection with a program of research carried out under his direction through contract NR 160-174 between the Office of Naval Research, Biology Branch, and the American Museum of Natural History, Department of Animal Behavior. Instruments used in this investigation were purchased through a grant from the Research Fund of the Council of the Scientific Staff of the American Museum of Natural History, and the photograph for Figure 1 was taken by Mr. R. E. Logan of the Museum's Photographic Division. Mr. James Zetek, custodian of the Canal Zone Biological Area, greatly aided in the arrangements. Dr. Schneirla was very helpful throughout the study and in the preparation of the manuscript. A preliminary report of this research has been published (Jackson 1952).

Methods

Air Moisture

A measure of air moisture was obtained with a highly portable, hand operated, aspirator-type psychrometer (Friez Model HA-2). Its small size permitted insertion into hollow logs or trees, small spaces under logs, or into subterranean cavities; but it was not an instrument of great precision. Periodic comparisons were made with a sling psychrometer, but no deviations were noted.

In determining the microclimate of a bivouac site, psychrometer readings were taken for several mornings following the emigration of a colony from the site at approximately the same time. Readings were also taken on the open forest floor several meters distant, and all observations were made between 1100 and 1200 hours (all time notations local standard time). The difference between the dry-bulb readings of the forest floor and the bivouac site ($\triangle$ dry bulb) was used as a measure of temperature; the difference in wet-bulb readings between the bivouac site and the forest floor ($\triangle$ wet bulb), as a measure of air moisture rather than relative humidity. The wet-bulb-depression statistic was used in this study since the temperature range over which the observations were made was very limited (25-28° C) and direct comparisons of these wet-bulb differences were possible with comparatively little distortion.

Temperature

For determining intra-bivouac thermal gradients, mercury-in-glass partial immersion thermometers (0-50° C, graduated in 0.2° C) were used. Supporting apparatus consisted of three aluminum rods that could be pushed into the ground a few inches from the bivouac (Fig. 1). A laboratory clamp on each rod held a guide stick (12" x ¾" x ¼") on the edge of which slid a thermometer. The set-up, with the guide sticks positioned just outside the bivouac wall, permitted the insertion and holding of thermometers at specific points within the bivouac.

FIG. 1. Apparatus for determining intra-bivouac thermal gradients. Thermometers, on guide sticks, are inserted in the bivouac. The thermograph for obtaining continuous records is shown with one sensitive element inserted from the back of the bivouac.

The procedure was to take a series of readings, using three thermometers, on the intersection lines of three horizontal planes (near the base, middle, near the top) with three vertical planes (near one side, middle, near the other side). The thermometers were inserted successively on each of the horizontal planes at intervals of 2.5 cm until the back wall of the bivouac was reached and were left in each position until equilibrium was attained (about a minute). Such series of readings were made at two hour intervals.

For obtaining continuous records of intra- and extra-bivouac thermal patterns, 2-pen Bristol thermographs (Model 2T531-1) were used. The sensitive elements, 7.75" x 0.375", permitted an instrument range of 15-42.5° C on a 9" chart and allowed chart readings to 0.1° C. One sensitive element was inserted into the bivouac center. The other was supported 2" off the ground by Y-shaped aluminum brackets in a niche similar to that of bivouac. With nomadic colonies, the instrument was set up each evening as the new bivouac formed and remained in place until the break-up of the bivouac the following evening. With statary bivouacs the procedure was similar; but the sensitive elements remained in essentially the same place (unless the bivouac shifted) for the whole observation period. The set-up was checked daily to make any necessary adjustments and to change the chart.

Instrument accuracy was checked periodically against A.S.T.M. bomb calorimeters in a water bath, but no instrument adjustments or data corrections were necessary. The same instrument was used for all observations on a given colony. In analyzing these data, chart readings every three hours were used as the basis for graphs. This was as satisfactory as calculating a 3-point moving average using hourly values.

Insertion of thermometers into the bivouac mechanically disturbed the ants somewhat; but unless the bivouac walls were thin or the ants hyperexcited, breaches in the wall around the thermometer were quickly filled in. However, the

thermograph probes were sufficiently large sometimes to produce a shifting away of the major portion of the bivouac. At other times the probe could be inserted so as to cause little disturbance, and the colony would remain clustered around the probe. Only records from this latter type of situation were used in the analyses.

Microclimate of Nomadic Bivouac Sites

The site of the nomadic bivouac may be described as "exposed" when the ants were clearly exposed to ambient conditions or "sheltered" when the bivouac was effectively shielded from such conditions. When data are summarized by these criteria and by two periods of the nomadic phase, a significantly greater ($P = 0.01$) percentage of bivouacs are located in "sheltered" sites during the last half of the nomadic phase than during the first half (Table I). The limited data collected during the rainy season showed no appreciable deviation from those of the dry season but are segregated in the tables for possible comparison.

Table I. Frequency of bivouac (temporary nest) establishment in various sites in relation to stage of the nomadic phase

Bivouac Site	Nomadic Days 2-9	10+
"Exposed"		
Beneath log	17 (3)*	18
Vines and brush	8 (3)	10 (2)
Tree base	6 (1)	3
Tree buttress	3	2
Plant base	3	0
Rock edge	2	0
Totals	39 (7)	33 (2)
"Sheltered"		
Hollow log	6	7
Base of hollow tree	5	4
Burrow	0	3
Palm frond	0	2
Totals	11	16
Percent "Sheltered"	19	31

*Numbers in parentheses refer to bivouacs established during the rainy season.

The bivouac, typically cylindrical in shape, is often modified by physical aspects of the environment. A "curtain" forms when the site has a partial wall, as the buttress of a tree or the side of a fallen log; a "compound" forms when brush or vines break the colony into several segments; a "plug" results when the colony fills in the opening of a hollow log or an animal burrow. Comparisons of the atmospheres of sites in which these various types of bivouacs occurred with ambient conditions indicate that compound and cylindrical bivouacs ocurred in "exposed" sites with approximately the same temperature and air moisture properties as the general environment (Table II). The curtain bivouacs occurred in more humid but still "exposed" sites. Plug bivouacs occurred in "sheltered" sites which were considerably cooler and moister than the ambient air.

Table II. Microclimatic characteristics of bivouac sites as related to bivouac types

	Bivouac type			
	Cylinder	Compound	Curtain	Plug
△ Dry Bulb* (°C)				
<0.50	9 (2)***	10 (5)	15 (4)	1
0.50 - 0.99	.....	3 (1)	8	6
1.00 - 1.49	.....	2	.....	5
1.50 - 1.99	.....	.....	1	3
Totals	9 (2)	15 (6)	24 (4)	15
△ Wet Bulb** (°C)				
<0.50	7 (2)	11 (6)	11 (4)	..
0.50 - 0.99	2	4	11	5
1.00 - 1.49	.....	.....	1	6
⩾1.50	.....	.....	1	4
Totals	9 (2)	15 (6)	24 (4)	15

*△ Dry Bulb = (dry bulb temperature of forest floor) - (dry bulb temperature of bivouac site).
**△ Wet Bulb = (wet bulb temperature of bivouac site) - (wet bulb temperature of forest floor).
*** = Numbers in parentheses refer to bivouacs occurring during the wet season.

During the latter portion of the nomadic phase a trend is apparent for the establishment of bivouacs in sites cooler and moister than the general environment (Table III). This trend is carried on into the statary phase where 66% of the bivouacs established during the dry season are in protected sites (Schneirla *et al.* 1954).

On the basis of these data a hypothesis could be built relating this trend to the microclimatic needs of the colony. As the brood approaches maturity and fills and perforates the bivouac, the maintenance of a stable internal environment becomes increasingly difficult. The movement into more protected sites would compensate for this instability and, during the quiescent statary phase, would afford increased protection to the colony.

However, an alternative hypothesis based on behavioral patterns which more adequately explains observations has been developed by Schneirla *et al.* (1954) and may be briefly summarized here. The new bivouac is initiated with the building of chains of workers quickly running down over other workers hanging head downwards from a surface and hooking tarsal claws. If this process progresses rapidly enough, chains broaden into ropes and reach the ground; and the bivouac framework begins to fill in.

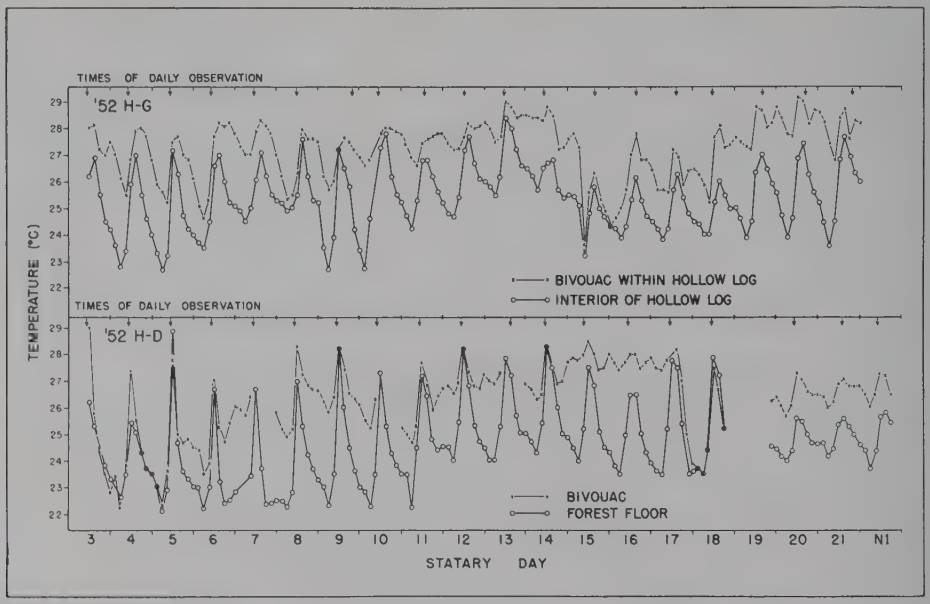

FIG. 2. Continuous intra- and extra-bivouac thermal patterns in two statary bivouacs.

TABLE III. Microclimatic characteristics of nomadic bivouac sites as related to temperature, air moisture, and stage of the nomadic phase

	Nomadic Days			
	2 - 5	6 - 9	10 - 13	14+
△ Dry Bulb* (C°)				
<0.50	9 (7)***	9 (4)	10	6
0.50 - 0.99	4 (1)	4	5	5
1.00 - 1.49	.....	2	4	2
⩾1.50	1	.....	..	2
Totals....	14 (8)	15 (4)	19	15
△ Wet Bulb** (C°)				
<0.50	10 (8)	8 (4)	8	3
0.50 - 0.99	3	5	8	7
1.00 - 1.49	.....	2	1	3
⩾1.50	1	.....	2	2
Totals....	14 (8)	15 (4)	19	15

*△ Dry Bulb' = (dry bulb temperature of forest floor) - (dry bulb temperature of bivouac site).
**△ Wet Bulb = (wet bulb temperature of bivouac site) - (wet bulb temperature of forest floor).
***Numbers in parentheses refer to bivouacs occurring during the wet season.

During the latter portion of the nomadic phase the threshold of excitability of the workers is at its lowest level with the larval brood large, active, and close to maturity. In this hyper-irritable condition, any disturbance, such as a slight breeze, is likely to disrupt the chain-formation process. Consequently, the strands and chains forming in protected sites are less likely to be disturbed and have a better chance of resulting in the reformation of the bivouac. Briefly, this appears to be the basis for the observed trend of late nomadic and statary bivouacs being established in more protected sites with a microclimate more favorable than that of the open forest floor. In addition, the fact that the bivouacs are re-established during the early night when temperature and air moisture differences between the various microhabitats of the forest floor are at minimum lends credence to this hypothesis.

BIVOUAC THERMAL PATTERNS

Statary Bivouacs

During the entire statary phase, the colony remains at the same site except for minor shiftings and is relatively inactive. On some days there is no raiding activity; on others, trails extend out for but short distances. The bivouac, commonly located in such protected sites as hollow logs or trees or animal burrows, is at a low excitatory level both because of greater insulation from such environmental stimulatory factors as sun flecks and drafts and because of reduced brood activity. This affords an opportunity to obtain continuous intra-bivouac thermal records, for the ants are less subject to movements away from the thermal probe.

Colony '52 H-G established its bivouac in one

end of a large hollow log. One thermograph probe was inserted into the bivouac; the other, supported within the log at at two meters' distance (Fig. 2). Probe insertion several times resulted in sufficient irritation to produce minor bivouac shifts, so that the sensitive element was left enclosed only by the bivouac margin. In one instance, the bivouac shifted to the opposite end of the log.

Despite this, several series of readings where the thermal probe remained well within the bivouac were obtained: S-11 to S-14 and S-18 to S-21 (*i.e.*, S-11 = eleventh day in statary phase). During such periods the intra-bivouac temperature was consistently several Centigrade degrees above the ambient temperature. Also, the intrabivouac temperature, with the ambient temperature, fell during the early morning hours, rose later in the morning, then decreased again during the afternoon, and then, in opposition to the ambient trend, rose in the evening. This was the pattern whether or not raids had occurred.

Colony '52 H-D, located under a partially hollowed log but not entirely protected from sun flecks and air movement, exhibited a similar pattern. Because of the more exposed location, the bivouac shifted several times early and again late in the statary phase. However, several satisfactory series of readings were recorded (S-12 to S-13), S-15 to S-17, and S-20 to N-1) and were quite similar to those of '52 H-G. Several breaks in the record resulted when the probe was removed to allow observations to be made.

During the day, even when there are no raids, some activity and consequent loosening of the bivouac structure occurs; and the intra- and extra-bivouac thermal patterns are similar, though differing by several Centigrade degrees. Following darkness, however, activity virtually ceases; the bivouac becomes more compact, a better insulating medium, and for several hours the heat earlier produced by the ants' activities is held. But by about midnight, thermal equilibrium is reached, and the intra-bivouac temperature slowly decreases.

Because of the size of the sensitive element, these data are but average temperatures of the whole bivouac. Just as the ambient temperatures are more variable and lower than these average intra-bivouac temperatures, the brood temperatures are less variable and are higher than the average bivouac temperature.

Nomadic Bivouacs

Diurnal thermal patterns within the nomadic bivouac were similar to those in the statory phase. Temperatures rose during the evening period of formation of the new bivouac as increasing numbers of ants clustered around the element, fell during the early morning, rose again with the morning warming of the environment, and fell during the afternoon cooling of the ambient air and the gradual reduction of the old bivouac.

Studies using the recording thermometers compared the average internal thermal patterns of bivouacs in several sites with those of comparable environmental niches. Temperature values were read from the charts at nineteen hourly intervals from 2400 through 1800 hours, the approximate period of bivouac existence (Table IV).

TABLE IV. Paired thermograph measurements of intra- and extra-bivouac temperatures during the nomadic phase, based on summations of 19-hour series

Bivouac Site	n*	N**	Intra-bivouac		Extra-bivouac	
			Mean (°C)	S.D. (°C)	Mean (°C)	S.D. (°C)
Under or against log.....	16	304	26.7	1.12	25.0	1.68
Brush pile or forest floor..	7	133	26.5	1.07	25.3	1.55
Base of tree or buttress...	11	209	26.6	1.11	25.3	1.68
Within log.....	4	76	26.5	1.33	24.2	1.37
Within log (Extra-bivouac: forest floor)...	1	19	26.5	1.10	25.5	1.69

*n = No. of 19-hour series.
**N = Total number of observations (n x 19).

Mean intra-bivouac temperatures at least 1° C higher and standard deviations about 33% less than the values of the corresponding environmental niches indicated a higher and more stable thermal environment within the bivouac. In the case where the bivouac probe and the reference probe were both within a hollow log, the intra- and extra-bivouac standard deviations were the same, but the intra-bivouac mean was more than two Centigrade degrees higher.

Thermal patterns in three horizontal sections through each of three representative bivouacs allow internal examinations of the nests. Early in the nomadic phase (Fig. 3), the hot core containing the brood is small and centrally located; and the bivouac as a whole is compact and exhibits a sharp thermal gradient to the ambient air. Midway through the nomadic phase (Fig. 4), the hot area has expanded; and with a more porous, looser bivouac structure, the thermal gradient is not as sharp. By the end of the phase (Fig. 5), when the mature larvae are distributed throughout the bivouac, the walls are very porous; and only a slight thermal gradient is present.

In these figures, the hatched areas represent portions of the bivouac above 29.0° C and not the brood areas *per se*. However, especially in Fig-

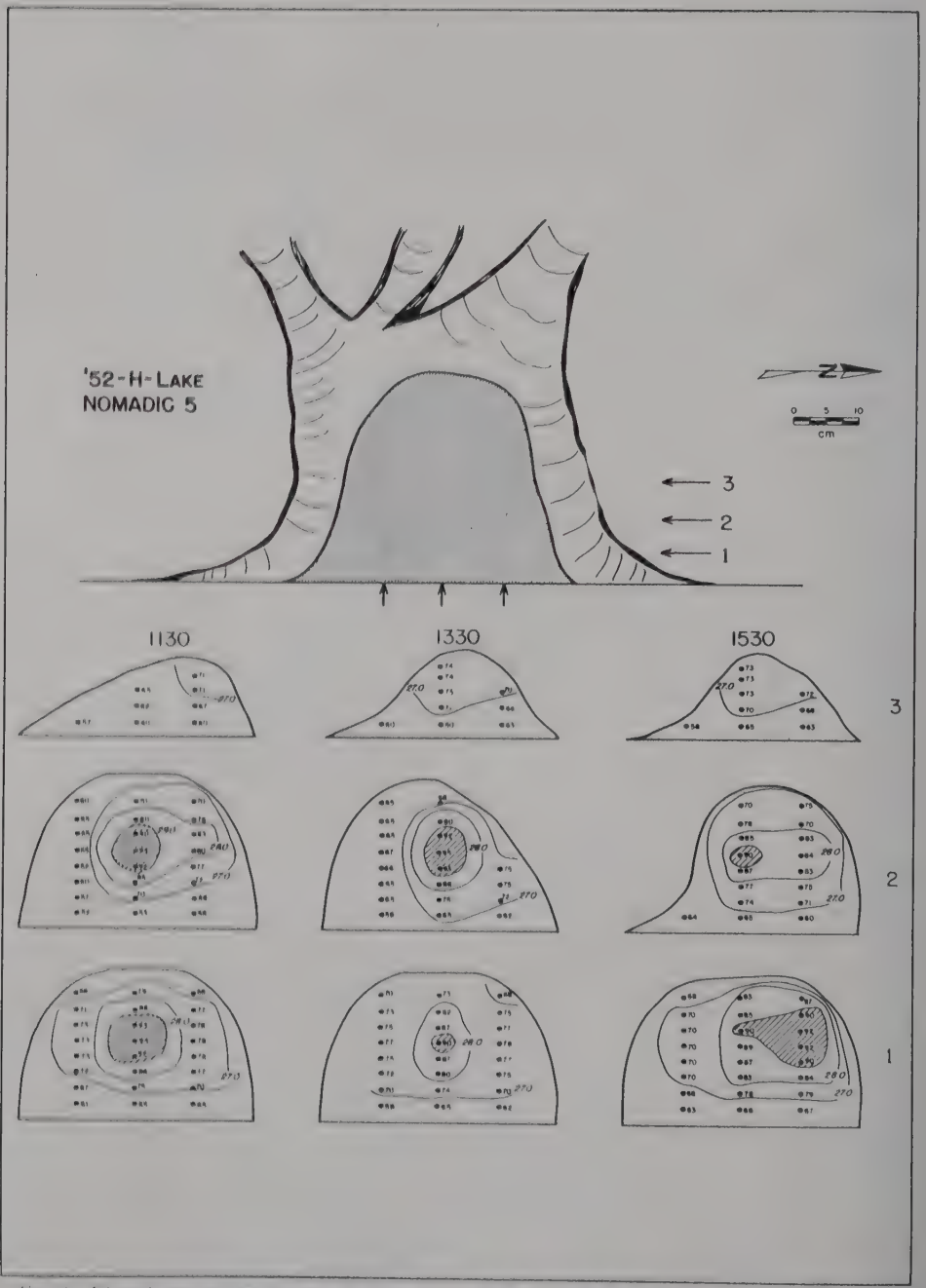

FIG. 3. Diurnal temperature patterns in three horizontal sections of an early nomadic bivouac. Isotherms are at intervals of one Centigrade degree.

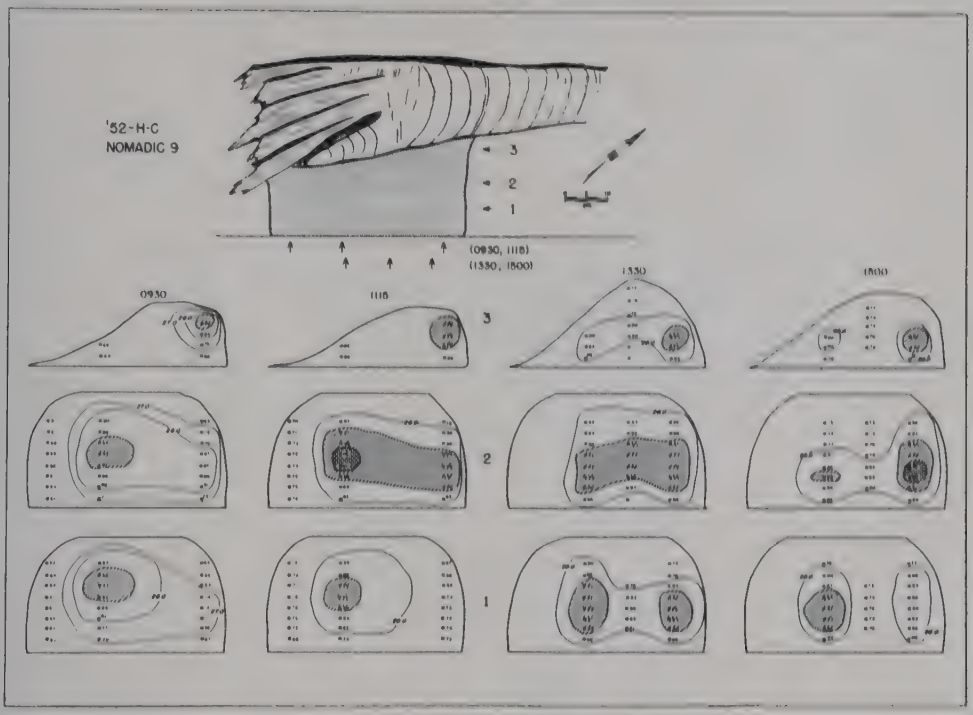

FIG. 4. Diurnal temperature patterns in three horizontals sections of a mid-nomandic bivouac. Isotherms are at intervals of one Centigrade degree.

ures 3 and 4, they do approximate the sites of brood concentration. Ambient temperatures may be closely approximated by taking the lower marginal bivouac readings.

In these patterns the effect of workers being drawn out into raiding trails and leaving peripheral portions of the bivouacs very porous is evident, especially in Figure 5. The basal portions are most commonly affected, but upper portions may also be reduced to strands if the bivouac hangs from several surfaces.

DISCUSSION

As in other social insects, the nest or bivouac of the army ant provides greater stability of environment and microclimate for the developing brood. This is true even on the relatively unvarying tropical forest floor. While there appears to be no specific response in the bivouac site selection process to the temperature-air moisture complex, the ants do respond negatively to air currents and direct radiation. As suggested by Schneirla *et al.* (1954), these account, at least in part, for the tendency to locate bivouacs in more sheltered sites (with less temperature-air moisture variation) during times when bivouac walls have been made porous by expanding brood and thus subject to greater desiccation and temperature fluctuations.

Thus the bivouac permits the army ant to be a highly mobile social insect by providing for the brood, and for the adult population as well, protection and insulation from the climatic variations without. Temperature variations of the young brood mass are slight; those of the bivouac, considerably less than the ambient conditions.

These data, though in general agreement with those of Schneirla *et al.* (1954), are not all directly comparable. For the most part, theirs are based on diurnal observations, mine are, in part, based on 19- and 24-hour series. Both series of data indicate the general intra-bivouac temperature to be 1-2° C above that of the environment and that of the compact brood mass to be several degrees higher still.

Since the observations of Schneirla *et al.* were terminated in early evening, the evening thermal upswing in the statary bivouac, characteristic of my records, was not noted. However, an indication of this occurs in their statary colony record (p. 285) just before the termination of observations. Their data also show the modified rise and

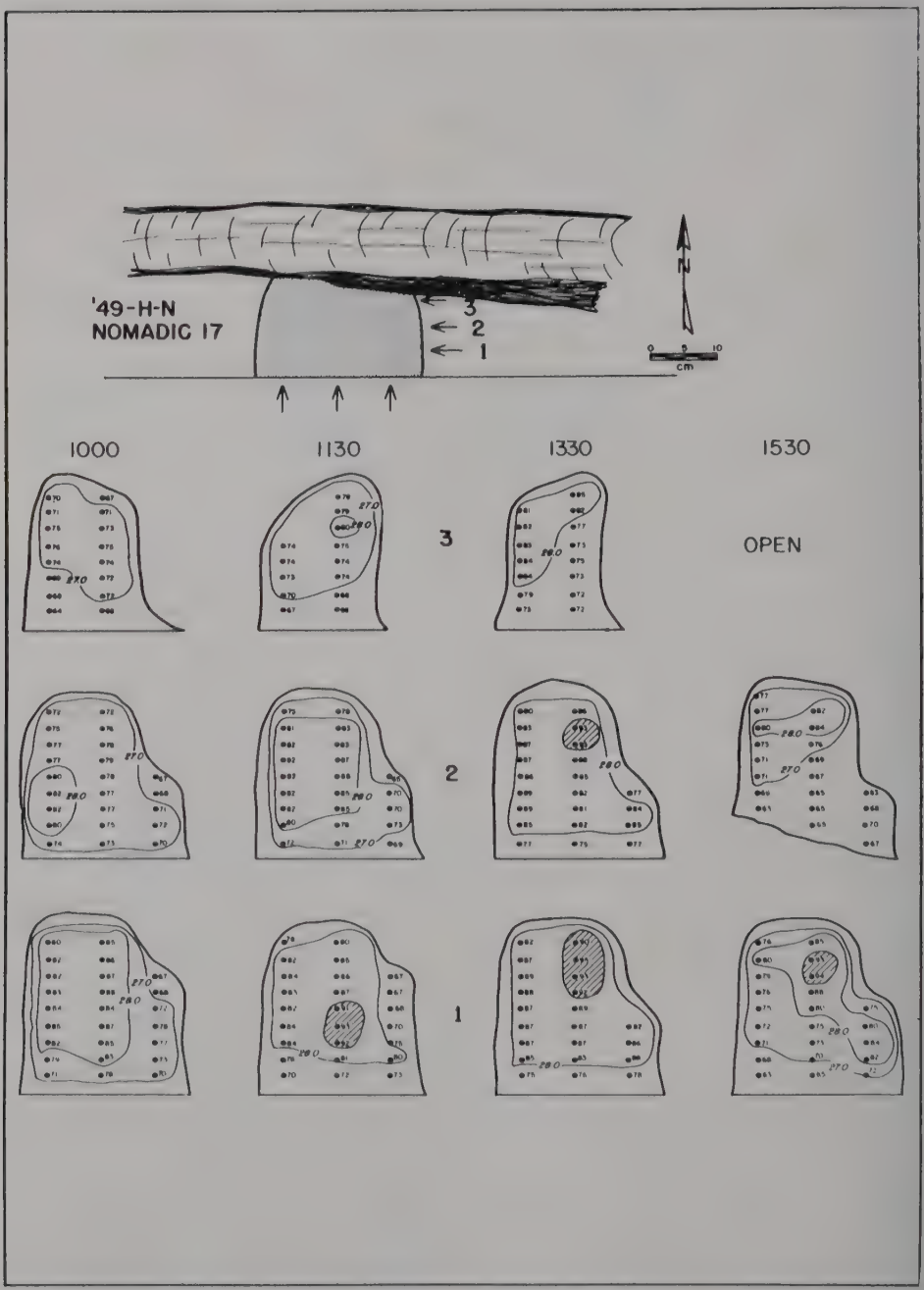

FIG. 5. Diurnal temperature patterns in three horizontal sections of a late nomadic bivouac. Isotherms are at intervals of one Centigrade degree.

fall of the intra-bivouac temperatures with the general diurnal pattern of the forest floor.

Summary and Conclusions

Studies of the bivouac or temporary nest of the army ant (*Eciton hamatum* Fabricus) in relation to its internal and external microclimate were made on Barro Colorado Island, Panama Canal Zone. Both nomadic and statary bivouacs, though following ambient temperature patterns, remained at least 1-2° C above the environmental temperatures and exhibited reduced amounts (⅓ smaller standard deviations) of fluctuations. Bivouac temperatures fell in the early morning, rose in the late morning, fell again in the afternoon, and, in contrast to the ambient temperatures, rose again in the evening.

Early nomadic bivouacs were compact with a sharp, radial thermal gradient. Late nomadic bivouacs were porous and with almost no gradient. Mid-nomandic bivouacs were intermediate.

A tendency for nomadic bivouacs to be located increasingly in cooler and moister sites as the nomadic phase progressed was observed. This appeared related to behavioral patterns and the mechanics of nest formation rather than a response to differing temperature-air moisture patterns *per se*.

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VEGETATION AND SOIL RELATIONSHIPS IN THE GLADE REGION OF THE SOUTHWESTERN MISSOURI OZARKS[1]

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Introduction

Extensive glade areas occur in the White River region of the Missouri Ozarks (Fig. 1). The vegetation of the "glades" is predominantly a grass cover with a scattering of cedar, *Juniperus virginiana*,[2] and scrubby hardwoods. Soils are shallow, overlying resistant beds of limestone. Horizontal outcroppings of rock occur at irregular intervals on slopes (Fig. 2). Moisture conditions in the surface soil vary widely, from saturation in early spring or immediately after rain to air dryness during summer dry periods. Many herbaceous species normally complete their growth and seed production before moisture deficiencies develop. The mean annual rainfall for one station is 43.7 inches, which equals or exceeds amounts for some of the more heavily forested areas of the eastern Ozarks (U.S.W.B. 1954).

Adjacent to the glades are areas of natural woodland. The transition from grassy, open conditions

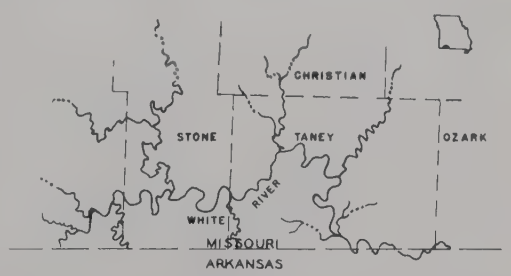

Fig. 1. The glade region, showing counties in which observations were conducted. Inset, upper right, indicates location in Missouri.

of glades to the relatively dense forest is frequently abrupt (Fig. 2). The forested areas are composed mainly of oak, Quercus, and occur on knolls and ridges immediately above the glades. These ridge-top landforms supporting forest growth are remnants of geologic strata composed of cherty limestone. The soil mantle has a high content of unconsolidated chert.

Many of the glade and forest plants are common to the Ozark region as a whole. Some species, as indicated by Steyermark (1940), are more local, perhaps even rare. Still others are related to a southwestern flora.

[1] Contribution from the Central States Forest Experiment Station, Forest Service, U. S. Department of Agriculture, and Missouri Agricultural Experiment Station, Journal Series No. 1642. Approved by the Director.

[2] Nomenclature is that of Fernald (1950), except for the Gramineae. For the grasses Hitchcock (1950) is followed.

FIG. 2. A representative glade site showing rock outcropping.

The nature of forest and glade vegetations and the generally narrow transition zone indicate that local soil conditions are limiting factors. In addition to their academic interest, the glades are valuable cattle grazing areas, and are important to the local economy.

This investigation, conducted by the University of Missoui and the Central States Forest Experiment Station, considers the following objectives: (1) determination of species composition by quadrat analysis of glades and adjacent forest growth of the ridges and hill tops (the more mesophytic forests of the broader uplands as well as the extensive forests of the valleys and drainages below the glades are not included in the present study, (2) phenological observations of major species, and (3) evaluation of critical soil factors in glade and forest sites.

VEGETATION OF THE GLADES

Representative glade sites were selected for plant collection, quadrat studies, and phenological observations. These sites were located in Taney County on the Mark Twain National Forest, T23N, R18W, section 12 and T23N, R17W, section 7. Some collections and seasonal observations were made in other glades of the county, as well as in parts of Stone, Ozark, and Christian counties.

Work was started in October 1952, and was continued through April 1955. Field observations were made approximately every 6 weeks from March to November of each year.

Frequency and cover estimates of species were determined from quadrat studies conducted during August of 1953 and 1954. Thus, not all vernal and ephemeral species were included; however, some identifications were possible from old growth or fruits. One hundred 1 x 1 meter quadrats were examined. Quadrats were spaced 15 meters apart along transect lines oriented across the contour. This method systematically covered the areas selected for quadrat analysis. The number of quadrats employed exceeded the five per cent minimal area requirement described by Cain (1938). Cover for each species in the plots was determined by visual estimate as a per cent of the total plant cover. Percentages were recorded for each quadrat, from which a species average was determined. Species were divided into dominance classes according to the classification presented by Cain (1932).

A grass flora predominated in the glades. The principal species of grasses made up approximately 78 per cent of the herbaceous plant cover. Little bluestem, *Andropogon scoparius,* occurred in 85 per cent of the plots and was the most uniformly distributed species. It was also the dominant species, comprising 51 per cent of the total herbaceous cover.

The annual "bald grass," *Sporobolus neglectus,* was another typical species of the glade. Average frequency was 49 per cent, although distribution was sporadic in any one glade. Frequently, this species was abundant on shallow soils where perennial grasses were sparse.

Other grass species that were dominant locally but generally lacking in uniformity of distribution within a glade included big bluestem, *Andropogon gerardi,* sideoats grama, *Bouteloua curtipendula;* switchgrass, *Panicum virgatum;* Indian grass, *Sorghastrum nutans;* prairie dropseed, *Sporobolus heterolepis;* and purple top, *Tridens flavus.*

The dominant grasses listed above flower in summer and fall. During the drouth years, 1953-1954, flowering occurred sparingly. Several species failed to flower. Flower production under the drouth conditions appeared most successful in sideoats grama and switchgrass. In 1955, with higher rainfall, flowering and seed production appeared normal in all species.

Effect of continued moisture deficiency on little bluestem, the principal glade species, was observed in quadrat studies. Plots indicated varying results, from no apparent damage to complete deterioration. Estimates of reduction in live crown basal area for the 10 quadrats along one transect from the lower slope to the crest of the glade were 35, 25, 40, 45, 100, 0, 10, 0, 25, and 10 per cent deterioration. The wide range in losses is attributed at least in part to edaphic variations, mainly soil depth.

Grasses infrequently distributed and each constituting less than one per cent cover included *Aristida dichotoma, A. oligantha, Bromus commutatus, Danthonia spicata, Eragrostis spectabilis, Festuca octoflora, Panicum capillare, P. flexile, P. huachuache, P. tennesseense,* and *Sporobolus asper.*

Soil moisture variations within glades were indicated by the variable flora. While site dryness, conditioned by shallow soil and rapid runoff, was a paramount ecological influence, subsurface drainage over bedded rock resulted in temporary seeps. Various mesophytic species, mainly members of the sedge family, *Cyperaceae,* occurred in localized areas under these conditions. Several carices, however, were less limited in distribution and occurred also in other parts of the glade. These were *Carex artitecta, C. hirsutella,* and *C. muhlenbergia.* On the rock outcrop over which seepage water flowed, a blue-green alga, *Nostoc,* prevailed in great abundance.

Quadrat frequencies were low for most other herbaceous species of glade vegetation. Sixty per cent of these species occurred in frequencies of 20 per cent or less. *Houstonia nigricans* although not abundant occurred most uniformly, having a frequency of 57 per cent.

Lace-leaf ragweed, *Ambrosia artemisiifolia,* and two species of croton, *Croton capitatus* and *C. monanthogynus,* were present in locally high densities. These three species are annuals, and spread noticeably during the drouth years. Frequency values for these annuals based on 1953 and 1954 quadrat analyses of the same sites are:

	1953	1954
	%	%
Ambrosia artemisiifolia	2	19
Croton capitatus	5	25
C. monanthogynus	5	45

The increase in *Croton* spp. has also been observed throughout the glade area, apparently correlated with drouth damage to other species, particularly the perennial grasses.

Conspicuous spring-flowering annuals were sandwort, *Arenaria patula; Leavenworthia uniflora,* and stonecrop, *Sedum pulchellum.* These occurred in dense colonies, but have only limited forage value. *Palafoxia callosa,* a widespread autumnal annual, was one of the last species to flower in the glades.

Seventy-six per cent of the herbaceous species in the glades were perennials, of which 62 per cent matured in spring or early summer. Only 19 per cent of the perennial grasses were spring bloomers. As stated previously, none of those grasses classified as dominants showed early growth or flowering development. The vernal aspect of the glades was composed chiefly of non-grass species. The grass flora did not gain aspect dominance until later in the season.

The principal tree species in the glades was eastern redcedar. It occurred in varying densities, some glade sites having only a scattering of individuals with others undergoing enclosure. Current invasion and spreading of the species are apparent. Decreasing incidence of severe fire is considered a contributory factor. Studies of similar vegetations in other regions indicate the sociological importance of eastern redcedar in limestone glade communities (Carr 1944, Erickson 1942, Freeman 1932, Harper 1926, Quarterman 1950). Other woody species found in the glades include *Acacia angustissima* var. *hirta, Andrachne phyllanthoides, Berchemia scandens, Bumelia lanuginosa, Ceanothus ovatus, Celtis tenifolia* var. *georgiana, Chionanthes virginica, Clematis versicolor, Cornus asperifolia, Cotinus obovatus, Diospyros virginiana, Ilex decidua, Juniperus virginiana, Rhamnus caroliniana, Rhus aromatica, R. copallina, Rosa carolina* var. *villosa, Smilax Bonanox, Ulmus alata, Vitis Lincecumii* var. *glauca.* With the exception of *Acacia, Andrachne, Bumelia,* and *Symphoricarpos,* these are spring-flowering species.

Forest Vegetation of the Knolls and Ridges

Frequency, density, and basal area for tree species were determined in the forest type identified with the chert knolls and ridges. The random pairs method (Cottam and Curtis 1949) was employed in the field studies; however, an exclusion angle of 180° was used for greater convenience. This method was easy and rapid and, under the conditions of study, was deemed suitable. No attempt was made to compare this method with other procedures. Studies in Oklahoma by Rice and Penfound (1955) and in Appalachian forests by Shanks (1954) have shown discrepancies in results when analyzed with data based on other methods. Recently, however, Cottam and Curtis (1955) have indicated corrections in the originally proposed calculation of mean area, when using the random pairs method.

Five sites were studied in the Mark Twain National Forest. Forty random pairs were observed in each, making a sample total of 400 trees with diameters four inches and greater. In addition, 40 milacre plots were sampled for all trees in the one- to four-inch classes in each of the five study locations.

The principal tree species of the forest adjacent to the glades were post oak, *Quercus stellata,* and black (Buckley's) hickory, *Carya texana.* Their combined density, including all size classes one inch and greater was 50.0 per cent of the stand total. Similarly, 70.6 per cent of the basal area was comprised of these two species.

TABLE I. Tree species in oak forest types. Frequency and density and square feet basal area expressed as per acre values

Species	Size Classes - inches d. b. h.									Total All Classes	
	1-3.9			4.0-9.9			10+				
	F%	D	BA	Frp %[3]	D	BA	Frp %[3]	D	BA	D	BA
Quercus stellata	60	128	1.72	48	49	15.52	15	10	8.10	187	25.34
Q. marilandica	42	40	0.48	10	12	1.79	....	..	....	52	2.27
Q. velutina	30	40	0.88	18	11	4.62	2	1	0.50	52	6.00
Q. alba	23	88	2.20	2	1	0.84	2	1	0.11	90	3.15
Q. muhlenbergia	12	16	0.35	2	3	0.22	..	..	....	19	0.57
Q. Schumardii var. *Schneckii*	..	..	....	2	1	0.25	..	..	....	1	0.25
Q. rubra	[4]	..	....	..	..	....	..	..	....	..	....
Carya texana	41	160	1.40	35	27	6.55	2	1	0.74	188	8.69
Diospyros virginiana	33	48	0.58	6	4	0.22	..	..	....	52	0.80
Sassafras albidum	12	56	0.30	..	..	....	..	..	....	56	0.30
Ulmus alata	4	20	0.44	..	..	....	..	..	....	20	0.44
U. rubra	[4]	..	....	2	1	0.11	..	..	....	1	0.11
Cercis canadensis	4	10	0.01	..	..	....	..	..	....	10	0.01
Cotinus obovatus	2	20	0.01	..	..	....	..	..	....	20	0.01
Fraxinus americana	[4]	..	....	2	1	0.25	..	..	....	1	0.25
Acer saccharum	[4]	..	....	..	..	....	..	..	....	..	....
Total	..	626	8.37	..	110	30.37	..	13	9.45	749	48.19

[3]random pair frequency. [4]observed outside study plots.

As shown in Table I, the stand densities of post oak and black hickory were similar; however, the latter species was more numerous in diameter classes between one and four inches. Few specimens were measured in excess of ten inches d.b.h., particularly of black hickory. For post oak, 68.4 per cent of the trees were less than four inches d.b.h.; 26.2 per cent between four and ten inches; and 5.4 per cent in larger classes. In comparison, percentage densities for black hickory in these size groupings were 85.1, 14.4, and 0.5. The proportionately greater representation of post oak in larger classes is illustrated by comparing basal area, which was 2.9 times that of black hickory. Importance values for post oak and black hickory in size classes four inches and larger based on percentage determinations of frequency, density and basal area (Curtis and McIntosh 1951) define them as principal dominants and codominants. The aggregate importance value of these two species was 215 out of a 300 stand total.

The remaining species were most numerous as small trees. In this group, only black oak, *Quercus velutina,* and white oak, *Q. alba,* occurred in sizes larger than ten inches; however, neither was frequent. In diameters between four and ten inches, black oak exceeded considerably the frequency and density of white oak. The former species, on the basis of relative abundance and representation of size classes, was ranked third in stand importance. Blackjack oak, *Quercus marilandica,* was the fourth principal species, being numerically equal to black oak but smaller in size. The four species, post oak, black oak, blackjack oak, and black hickory, were also indicated as dominants and secondary species in oak types of the forest-prairie transition of Oklahoma (Rice and Penfound 1955).

Black oak and white oak increased in size and prevalence with increasing distance from the glade conditions, as the degree of exposure lessened and soil depth increased. Sugar maple, *Acer saccharum,* and northern red oak, *Quercus rubra,* while present in the peripheral forest, were relatively unimportant in species structure of the stand. Quantitative data for all species are recorded in Table I.

Other forest subdominants included *Bumelia lanuginosa, Celtis tenuifolia* var. *georgiana, Chionanthese virginica, Cornus florida, Ilex decidua, Juniperus virginiana, Prunus serotina,* and *Viburnum rufidulum.* These species were generally infrequent and were never abundant. *Bumelia, Celtis, Chionanthes, Ilex,* and *Juniperus,* the latter particularly, prevailed in high densities in several glades (Fig. 3).

The shrub flora included the locally abundant aromatic sumac, *Rhus aromatica,* and buckbrush, *Symphoricarpos orbiculatus.* Shrub or shrub-like species of lesser frequencies and densities were *Acacia augustissima* var. *hirta, Ceanothus ovatus,* and *Vaccinium* spp. The genus *Vaccinium* occurred in the forested area but did not extend into the typical glade habitat.

The vine flora in the oak woods type included the herbaceous species, *Passiflora lutea,* and several representatives of the Vitaceae, *Cissus incisa, Vitis aestiva'is,* and *V. Lincecumii* var. *glauca*

FIG. 3. The eastern redcedar, *Juniperus virginiana,* enclosing a glade.

The grasses constituted an important component of the herbaceous ground cover in forest sites. *Danthonia, Muhlenbergia,* and *Panicum* were represented most frequently. Other genera less frequent were *Agrostis, Andropogon, Bouteloua, Bromus, Elymus, Festuca, Hystrix, Poa, Sporobolus, Tridens,* and *Uniola.* The genus *Panicum* was most significant. It had the largest number of species, many of which were restricted to the forest zone. As shown previously, only a limited number of *Panicum* spp. occurred in the glade. No one species of the genus was frequent or abundant. *Danthonia spicata* was a singularly prominent species in the dry woods type.

Other principal herbaceous groups in forest sites included the Leguminosae and Compositae. In the former the most common genera were *Desmodium* and *Lespedeza. Lespedeza repens, L. violacea, L. virginica* and *Desmodium rotundifolium* were most prevalent. Characteristically, these genera and also goat's-rue, *Tephrosia,* were less frequently represented in glade habitats. *Desmodium* spp., *Lespedeza repens* and *L. violacea* did not occur in glades. Species found in oak woods which were equally or more frequent in the glades were Korean lespedeza, *Lespedeza stipulacea;* prairie clover, *Petalostemum purpureum;* scurf pea, *Psoralea psoralioides* var. *eglandulosa;* pencil-flower, *Stylosanthes biflora;* and sensitive-brier, *Shrankia Nuttallii.*

Other characteristic elements of herbaceous vegetation in the oak woods type included *Antenanria, Aster, Coreopsis, Heliopsis, Solidago,* and *Verbesina,* all of the Compositae. Highest frequency of occurrence in this group was noted for *Antennaria,* while other genera were sporadic in distribution.

EDAPHIC RELATIONSHIPS

Soil depth was considered a critical determinant of soil moisture availability and root penetration. Since these factors had an important influence on species distribution between glade and forest sites, as well as in the glade itself, more than one hundred soil borings were taken to determine average depth to bedrock. Boring locations in both glade and forest sites were determined by pacing a line across the contour. Sampling was not difficult in the glade because of shallow depths. Considerable difficulty was encountered in forest sites, however, where the soil had a high content of chert fragments. Furthermore, the average depth to bedrock was considerably greater, being two or more feet in most cases.

Soil samples were taken in 1954 to determine soil acidity, maximum capillary moisture and permanent wilting percentage. Three soil levels were sampled under forest, a surface horizon, a subsurface which appeared somewhat leached, and a dense clay zone. The latter usually varied from 12 to 18 inches below the surface, and was sampled arbitrarily to 36 inches whenever conditions permitted. The general thinness of glade soils, and the lack of horizon development dictated a single zone sampling.

Standard procedures were followed in the soil analyses. Free acidity was determined with a pH meter. Capillary moisture measurements were made in the laboratory using replicated, air-dried samples. In determining wilting percentages, sunflower plants were grown for approximately five weeks at which time containers were sealed and watering was terminated. Moisture calculations were based on oven-dried weights. The soils of Taney County, where observations were made, have been surveyed and described by Scrivner and Frieze (1953). In the present study soil depth measurements and evaluation of moisture constants indicated primary differences between glade and forest sites. A characteristic feature of glade soils was shallow depth. The average depth was 4.8 ± 3.93 inches. The range in depth as measured across the contour varied from zero on an outcrop to 18 inches. A typical transect in the glade showed the following depths of soil in inches, and will serve to explain the large deviation about the mean: 2, 12, 6, 2, 16, 3, 1, 0, 3, 3.

Soil depth was greater in forest sites than in the glades. Scrivner and Frieze found an average depth to bedrock of four feet or more. Their survey, however, was not limited to the marginal forests. In the present study, measurements were taken to three feet although greater depth to bedrock did occur. Shallower depths were also found, in some instances less than two feet.

Variations in soil conditions of the region are associated with dissimilar parent materials of

Ordovician origin (Branson 1944). The forested knolls and ridges above glade positions are identified with limestones having a high content of chert. Under conditions of weathering and solution of limestone the soil mantle, classified in the Bodine series, is cherty and has developed to a depth of several feet. The glade slopes occur below the forest in physiographic position, and are formed from a siliceous, magnesium limestone relatively resistant to weathering. The soils are typically shallow, underlain by bedded rock, and are less cherty than those derived from more readily weathered limestones supporting forest growth. These are designated as glade-rock soils.

Some differences in moisture constants were found in forest and glade soils. Wilting percentages of glade soils averaged 38 per cent less than those of forest surface soils, indicating a lower moisture-retention ability. Capillary capacities, however, were not significantly different. In the subsurface zone, in which a degree of leaching was evident, the capillary capacity and the wilting percentage was lower than in the surface horizon. Capillary capacity was 30 per cent less, and wilting percentage was reduced 14 per cent. Moisture constants increased sharply in the forest subsoil indicating a heavy retentive zone. These higher moisture values in the subsoil in addition to greater soil depth provide a larger moisture-holding capacity. Compared to glade conditions, drouth susceptibility is lessened by increased depth and a more favorable medium is provided for forest growth. A comparison of average moisture values follows:

Soil Type	Capillary Capacity—%	Permanent Wilting—%
1. Glade	16.0	6.9
2. Forest		
surface	17.8	11.1
subsurface	12.5	9.6
subsoil	26.1	21.6

Surface soils under forest were more acid than those in glade habitats. The average pH of the former was 6.5 compared to 7.8 for glade sites. Although the variation was not great, the trends in acidity were consistent. Differences in geologic origin of soils and variations in humus types are possible factors. The restriction of oxylophytes such as *Vaccinium* spp. to cherty, forest-developed soils may also be correlative.

Summary

1. Species composition and ecological relations were investigated in local forest-glade transitions of the southwest Missouri Ozarks.

2. The forest vegetation was a xerophytic oak type separated by generally narrow ecotones from glade-prairie communities.

3. Principal species of the peripheral forest were *Quercus stellata, Q. marilandica, Q. velutina,* and *Carya texana. Quercus stellata* and *Carya texana* occurred most frequently. A varied subdominant flora was present, including oxylophytic *Vaccinium* spp. which were restricted to forested, chert-soil habitats.

4. Herbaceous plants typical of the forest ground flora were *Danthonia, Muhlenbergia, Panicum* with numerous representatives, *Desmodium, Lespedeza* and various Compositae genera.

5. Numbered among the glade dominants were *Andropogon* spp., *Bouteloua curtipendula, Sporobolus* spp., *Panicum virgatum* and *Sorghastrum nutans. Andropogon scoparius* was the principal dominant; *Sporobolus neglectus* was generally frequent and locally abundant.

6. In the glades, *Juniperus virginiana* was the most frequently occurring woody species. Other typical woody plants were *Cotinus obovatus, Ilex decidua, Rhamnus caroliniana, Bumelia lanuginosa* and *Diospyros virginiana. Rhus aromatica* was the most common shrub.

7. Studies of the principal glade perennial, *Andropogon scoparius,* indicated a varying degree of drouth injury. The annual species, *Croton capitatus, C. monanthogynus,* and *Ambrosia artemisiifolia,* became more frequent in the glade habitat during the drouth period.

8. The development of forest and glade types is physiographically associated with differing geologic formations. Variable composition and rate of weathering of the parent material have produced soils with different characteristics. Soils in the glades are drouthy and shallow. The residual mantle supporting forest growth has weathered to greater depth and is more retentive of moisture, particularly in subsoil levels.

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THE USE OF COVER AND FREQUENCY IN THE DETECTION OF PATTERN IN PLANT COMMUNITIES

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Introduction

Various workers (Blackman (1935), Clapham (1936), Archibald (1948) etc.) have made it clear that individuals are rarely distributed at random within a plant community. Although non-randomness can sometimes be explained by the biological characters of the species concerned (Ashby 1948) there are many cases which cannot be accounted for in this way. Greig-Smith (1952) has suggested that phases of a dynamic system of the type postulated by Watt (1947) may be characterized by differences in abundance of the same species, giving a mosaic of different density levels; this would again result in a non-random distribution. Whatever the cause of non-randomness, a knowledge of the scales of heterogeneity concerned—whether defined clumps or patches of different density levels—is essential to a further understanding of the phenomenon. Greig-Smith (1952) has described a method depending on analysis of density in a grid of contiguous quadrats the data from which are associated into successively larger blocks, a technique of considerable importance and value. Mean square plotted against block size shows a peak at the block size corresponding to the mean size of clump or mosaic unit. The method, based on trials with artificial communities, has proved satisfactory in the field (Greig-Smith 1952 (b), Phillips 1954).

Greig-Smith (personal communication) has used frequency data, in the form of the numbers of sub-units occupied in a grid unit, in the same manner as density data. The writer, in the course of an investigation into changes in community structure in upland Agrostis-Fescue communities, wished to determine the scales of heterogeneity associated with each species. Since in such a community the use of density data is impracticable due to the difficulty of distinguishing individuals, the frequency method was adopted. The grid method as hitherto used makes the implicit assumption that the areas of heterogeneity are isodiametric, but since the communities resulted from ploughing and reseeding it was suspected that areas of heterogeneity might be elongated in the direction of cultivation. If this is the case, the grid method as it stands is inadequate for this problem. Confirmation of this fact that the areas of heterogeneity were not isodiametric in the site examined was obtained by associating single grid units into blocks of 2, 8, 32, etc. in two ways (see Fig. 1).

For the majority of species, analysis of the same data, grouping the units in these two ways, showed a shift of peak in the variance curve to the right, when the long axis of the groups was at

[1] The author wishes to express his thanks to Mr. P. Greig-Smith under whose supervision this work was carried out, and to Professor M. S. Bartlett for his helpful criticism. I would also like to thank Professor P. W. Richards for providing facilities in the Department of Botany, and Derbyshire Education Committee for financial assistance during the period of this work.

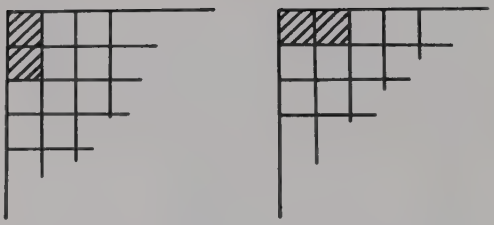


FIG. 1. The dimensional association of single grid units (see text).

right angles to the contours of the site. A method of analysis is clearly needed in this case that will describe the units of heterogeneity in terms of their linear dimensions, rather than in terms of mean area. The following technique offered a possible method of analysis.

In any one row or column, the individual grid units are grouped together linearly to give block sizes of 2, 4, 8, 16, etc. units; a separate analysis being carried out of each dimension of the grid. The maximum linear block unit obtainable, (i.e. the length of side of the grid) is not included in the graph of mean square against block size, as it does not give a true indication of heterogeneity at that scale. Such maximum block units are complete rows or columns, and their variance could be markedly influenced not only by heterogeneity in the direction under investigation, but possibly also by heterogeneity in the direction at right angles to it. This may be seen by consideration of a pattern such as Fig. 2. Here, a significant difference would be found between the columns, due, not to "linearity" of the areas of heterogeneity, but to the spatial distribution of the areas themselves. Such extreme regularity is unlikely to be found in the field, but the possibility of such an effect being even partially present makes it impossible to interpret inter-column differences in terms of heterogeneity of that scale.

It is to be expected that a partitioning of mean square values into two dimensional fractions will result in less pronounced peaks at the mean dimensions of the areas of heterogeneity, and frequently the "peak" will be merely a well defined change in the slope of the curve. The determination of the significance of any apparent peak presents a difficult problem. Once non-randomness has been established (and for most species randomness would be the exception) the classical variance ratio test no longer necessarily applies. Thus it would not be legitimate to test the increase in variance from one block size to the next in this way (Bartlett, personal communication), though it would separate out obvious sampling irregularities as non-significant fluctuations.

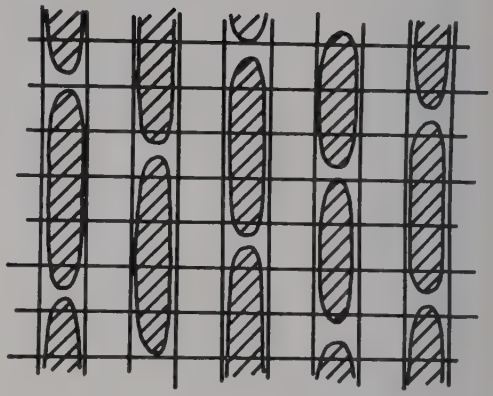


FIG. 2. Diagram illustrating possible spurious scale of heterogeneity if intercolumn differences are used in analysis (see text).

Thompson (1955) has discussed the problem and demonstrated the need for a valid test under the non-random conditions existing in most communities. For a model community of defined pattern he calculates the expected mean squares and respective standard errors for each block size, so that the set of expected mean squares for a given model has appropriate to it "significance bands" outside which terms observed from samples of the model would only be expected to fall with a given (small) probability. Thus if the calculated mean squares from observed data fall entirely within the significance bands of a model community, the model may be regarded as a valid description of the observed community.

In the absence of any exact test in the generalised case it is of value to apply the classical variance ratio test, to give an indication, at least, of the true level of significance of any peak, but such results must be treated with extreme caution. Usually the problem will resolve itself into a subjective assessment of "significant" peaks. When the difficulties of adequate sampling in the field are considered, the necessity of this final subjective approach is not surprising; accordingly a series of artificial models were used to evaluate this technique. At the same time the possibility of using cover rather than frequency as a measure of the abundance of a species was considered. A variance ratio test has been applied to adjacent block sizes and the "significant" peaks (5% probability level or less) on each curve are shown in the figures, to serve as a guide to the true level of significance.

METHODS

For the purpose of the investigation, clumps of individuals were represented as elongated oval

areas of 100% cover, laid out on graph paper with their long axes orientated in a vertical direction. The positioning of each clump presented a difficulty in that the layout of clump centres should be as random as possible, yet having no two clumps overlapping. It has been pointed out (Cottam, Curtis, and Hale 1953) that results obtained from communities with a low density of individuals have a markedly high standard error. Furthermore, the use of random co-ordinates to determine the centre of a clump, gave a considerable amount of overlapping even when the cover was still low. Thus in general the layouts finally constructed were not of randomly placed, but of underdispersed clumps. Pairs of co-ordinates were taken from a table of random numbers to determine clump centres; all co-ordinates which placed a second clump within one grid unit of another clump were ignored. A point was finally reached where nearly all the random co-ordinates taken, placed a clump in an overlapping position, and it was necessary to place the last few clumps in any unoccupied space remaining. This led to the introduction of an unknown amount of non-randomness, but the results were generally satisfactory. A layout with a low percentage cover was obtained by placing random centres until a clump fell in an overlapping position, this clump was ignored and no further ones added. This layout was to test the effect of low density on results.

An artificial pattern at different density levels was prepared by dividing the layout into a mosaic of roughly equal areas, each being designated as a low, medium or high density area. In order to establish the position of clump, pairs of random coordinates were taken for each density level and any point not falling in the area in question was ignored. The resultant numbers of random points falling in each class was as follows: high density areas (104 points), density per unit area 1.1950; medium density areas (48 points), density per unit area 0.5834; and low density areas (19 points), density per unit area 0.2188. The mean width of mosaic unit was 2.48 grid units.

Clumps of width $\frac{2}{5}$ units and length 2 units, were associated with each random point and the analysis carried out in the direction of clump width only. This small size of clump was selected to avoid any possible confusion of clump width with mosaic width.

In all layouts a strip of 2 grid units was allowed on the margins, which was ignored in the actual sampling. By this means it was hoped to eliminate the more serious marginal aberrations common to artificial layouts. The dimensions of a clump are expressed in terms of grid units. The following layouts were used in the 6 experiments: (1) clumps of size 1 x 2 grid units, placed at random (7.33% Cover); (2) clumps of size 1 x 2 grid units, underdispersed (20.71% Cover); (3) clumps of size 1 x 4 grid units, underdispersed (24.54% Cover); (4) a double scale of pattern—clumps of size 1 x 2 grid units, underdispersed; associated into random 8 x 8 groups (9.17% Cover); (5) a double scale of pattern—clumps of size 2 x 4 grid units underdispersed; associated into random 16 x 16 groups (8.62% Cover); (6) mosaic pattern of different density levels (15.80% Cover).

In the frequency analysis each grid unit was divided into 25 sub-units and the number of sub-units occupied was counted and expressed as a percentage. Unless otherwise stated, the size of grid used was 32 x 32 units, each unit being 0.5 inches x 0.5 inches (1.27 cm. x 1.27 cm.).

The adaptation of the technique for the analysis of cover data follows directly by replacing the rows and columns of a grid by line transects. Cover readings are taken at regular intervals along each transect, and the single readings are grouped together into basic units of 5 points, the percentage cover being recorded for each unit. The units are then grouped together into larger block sizes in the normal manner. In the experiments, random numbers were used to locate the origin of each transect, and cover readings were taken every 0.1 inches (0.254 cms.) along the length of each, giving a basic unit length of 0.5 inches (1.27 cms.).

In both methods the percentage frequency or cover readings were subjected to an angular transformation before analysis. The following notations have been adopted:

Analysis of rows is denoted as $(\rightarrow)$
Analysis of columns is denoted as $(\downarrow)$
Block size is abbreviated to N_s

Results

The frequency data in the analysis of experiment 3 $(\downarrow)$ (Fig. 3) show a sharp rise of mean square value to $N_s = 4$, and thereafter a non-significant increase and decrease to the higher block sizes. Similarly in the analysis $(\rightarrow)$ there is a clear cut peak at $N_s = 1$, followed by non-significant fluctuations in the curve at larger block sizes. Both peaks correspond with the size of clump used in the experiment. The cover data for the same layout (Fig. 6) follow a similar pattern, and in general, the results of cover and frequency analyses show very close similarity.

The results obtained from experiment 1 (Figs. 4 and 7) are anomalous in that there is consider-

able exaggeration of the true clump dimensions; this is a reflection of the low density of the layout, and a disadvantage which can be overcome by adequate sampling (see below). Similar considerations apply to the analysis (→) in experiment 2 (Figs. 5 and 8) where there is again an exaggeration $N_s = 2$ of the true dimensions of the clump width (1 grid unit). It is reasonable to suppose that, since a relatively large number of clumps overlap into 2 units of grid, an analysis of an area of heterogeneity of width 1 grid unit will show a peak at $N_s = 2$ and not at $N_s = 1$. This would not occur if the density of individual clumps were fairly high, although the effect could be overcome by taking a large sample of the community or by using smaller basic units. This is borne out by experiment 3 which has a much higher density of clumps and shows a sharp peak at $N_s = 1$ (24.54% cover as opposed to 7.33% cover in experiment 1).

The peak at $N_s = 8$ in the analysis (↓) of experiment 2 (Figs. 5 and 8) though not statistically significant is probably an indication of an unknown amount of heterogeneity introduced by positioning some of the clumps by hand as mentioned previously. This is more clearly shown in the cover analysis (Fig. 8), an indication, perhaps, of the greater sensitivity of cover, as opposed to frequency, as a measure of abundance. The more clearly defined peak in the analysis (↓) of experiment 3 (Figs. 3 and 6) at $N_s = 4$ compared with the peaks in figs (4, 5 and 8) suggests that the optimum size of basic unit is half, or less than a half, of the dimensions of the area of heterogeneity. The double analysis in experiment 4 (Figs. 9 and 10) clearly demonstrates this point; the density of clumps is low and the analysis (4a) is very unsatisfactory (Fig. 9), yet with a reduction of basic unit size in an analysis (→), more clearly defined peaks appear at $N_s = 4$ and $N_s = 16$ corresponding to the true double scale of pattern present, of 2.5 grid units and 20 grid unit groups, relative to the reduced grid units. Furthermore, since a reduction of grid unit size in a fixed area gives conjointly an increase in sample size, it is interesting to note that, using a quarter of the available data for analysis, there are again peaks in the expected positions (Figs. 10a and b).

The cover analysis (→) in experiment 5 (Fig. 11) again an experiment using a double scale of pattern shows a fairly clear-cut primary peak, though the percentage cover of the layout is low. The secondary peak appears at $N_s = 32$ instead of $N_s = 16$; this can only be accounted for by the fact that there is only a small number of clump aggregations, all of which actually overlap into the larger block size on analysis. The results for experiment 6 are clear cut showing the peak in the expected position (Fig. 12).

Sampling experiments

The unreliability of the results obtained from communities of low percentage cover necessitated further information on the relative effects of percentage cover and size of basic unit. Accordingly a series of artificial communities were used to obtain information on the sensitivity of the method at varying levels of percentage cover, using different sizes of sample and basic unit.

Four layouts were used, having approximate percentage covers of 5%, 10%, 15% and 20% respectively, the method of preparation of each being identical with that of the previous experiments.

For convenience transects were taken in a single dimension only; 8, 16 and 32 transects were used to compare the effects of sample size, and a basic unit of both 1 and 2 units, relative to clump width, was used in each case.

Results with basic unit equal to clump width

The results from the 5% and 10% layouts (Figs. 13 and 14) show the drift of peak to $N_s = 2$ previously mentioned, the peaks being more clearly defined with both increase of sample size and increase of percentage cover. In the 5% layout, the results using 8 and 16 transects (Fig. 13) are not satisfactory, as is to be expected from the small sample size, though the latter does show a tendency to peak at $N_s = 2$.

At higher percentage cover (15% and 20%), the size of sample does not seem to affect to any great extent the position of the peak (Figs. 15 and 16). It is interesting to note that the drift to the right is cancelled out as was previously predicted, and the "peak" appears at $N_s = 1$ with non-significant fluctations of the curve at larger block sizes.

The flat nature of these results under field conditions would be difficult to interpret since there is no exact test available of the possible significance of $N_s = 1$. Heterogeneity at this level in most cases would be due to the actual size of the individual, and if there is a suspected peak at $N_s = 1$, then a visual inspection of the area under investigation would readily confirm the likelihood of such a peak.

Results with basic unit equal to half clump width

In the 5% layout the smaller sizes of sample (8 and 16 transects) give an accurate detection of the true scale of pattern. The further increase of sample size to 32 transects gives a "flattening"

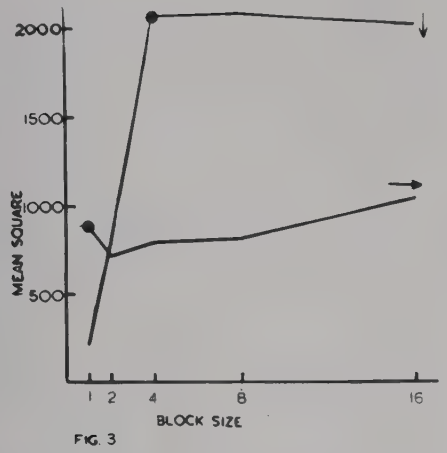


FIG. 3

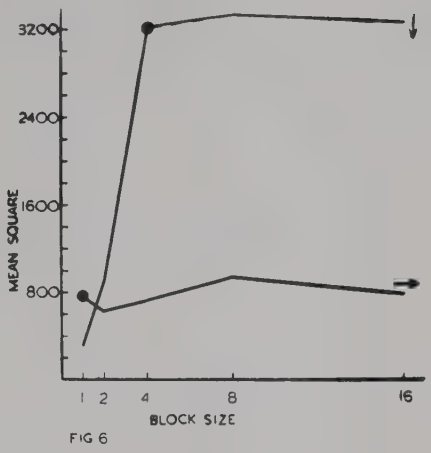


FIG 6

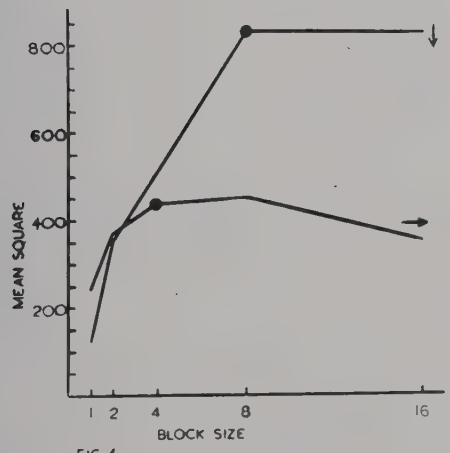


FIG. 4

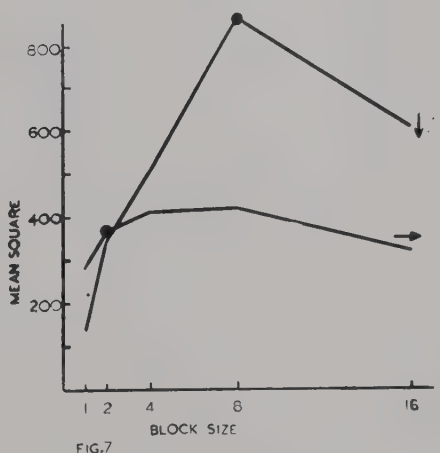


FIG.7

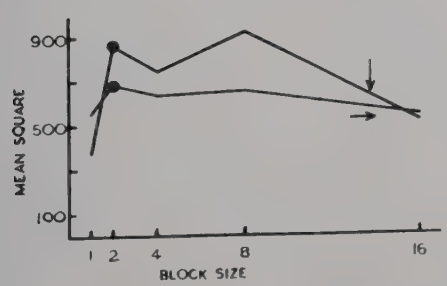


FIG. 5

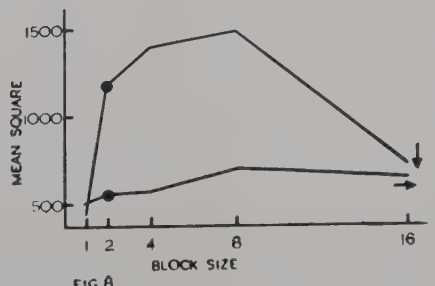
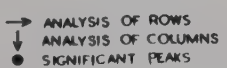


FIG. 8



FIGS. 3-8. Mean square plotted against block size.
FIG. 3. Frequency data, and Fig. 6, cover data for expt. (3).
FIG. 4. Frequency data, and Fig. 7, cover data for expt. (1).
FIG. 5. Frequency data, and Fig. 8, cover data for expt. (2).

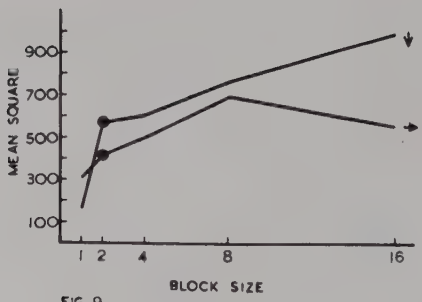


FIG. 9

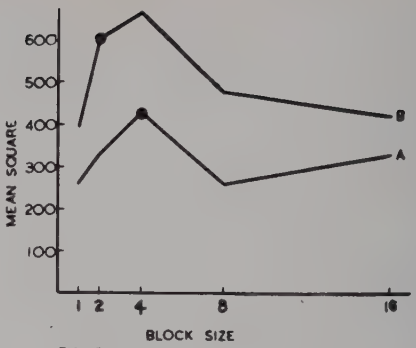


FIG 12

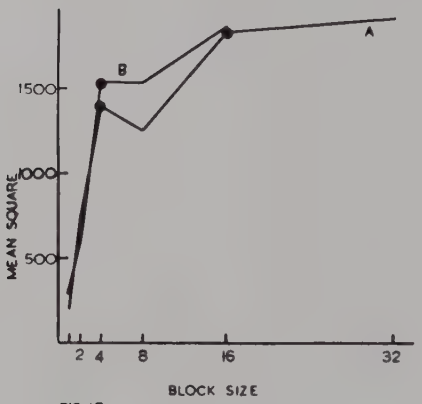


FIG. 10

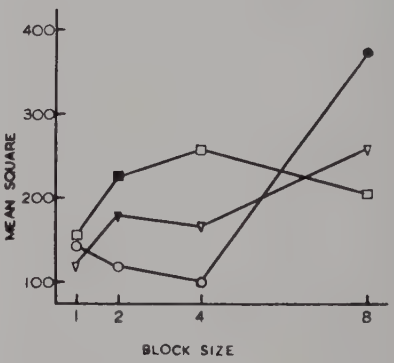


FIG. 13

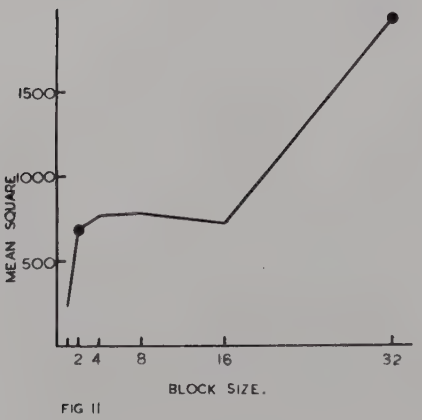


FIG 11

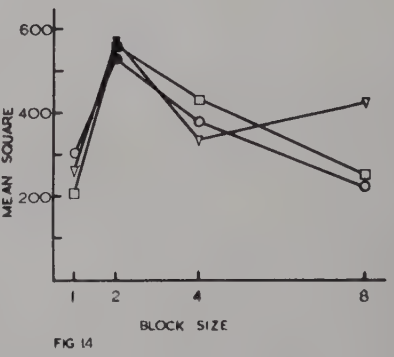


FIG 14

→ ANALYSIS OF ROWS. ○ 8 TRANSECTS.
↓ ANALYSIS OF COLUMNS □ 16 TRANSECTS
●▼■ SIGNIFICANT PEAKS. ▽ 32 TRANSECTS.

FIGS. 9-14. Mean square plotted against block size.

FIG. 9. Frequency data for expt. (4a).
FIG. 10. Frequency data for expt. (4) using reduced basic unit, A = total data, B = ¼ of data.
FIG. 11. Cover data of expt. (5).
FIG. 12. Frequency (A) and Cover (B) data, of expt. (6).
FIG. 13. Cover data of the 5% layout.
FIG. 14. Cover data of the 10% layout.

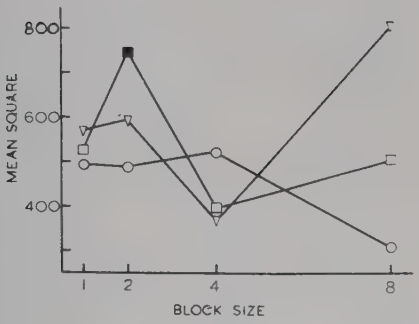


FIG. 15

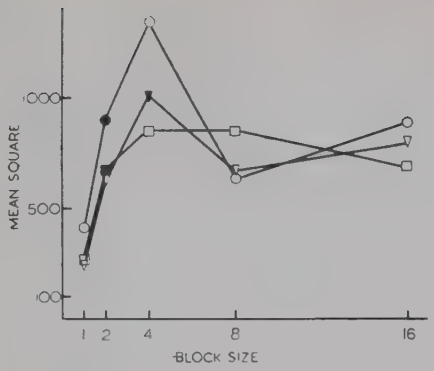


FIG 18

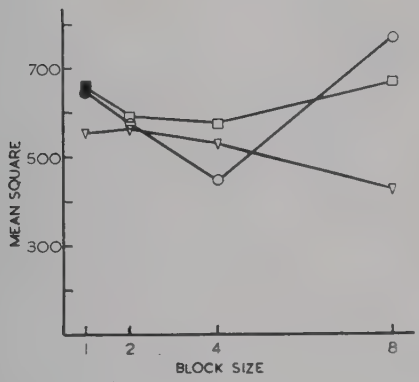


FIG. 16

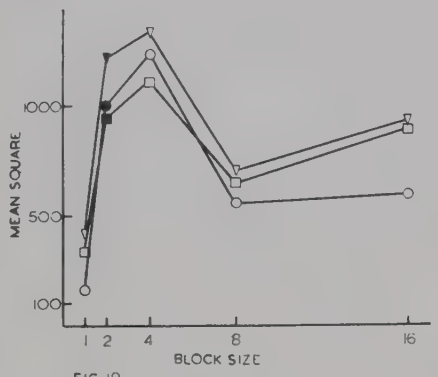


FIG. 19

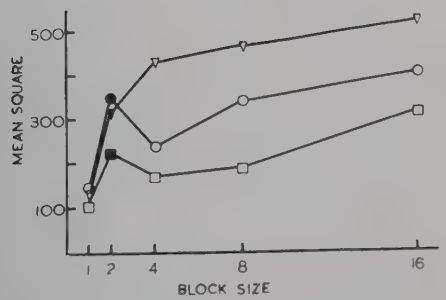


FIG. 17

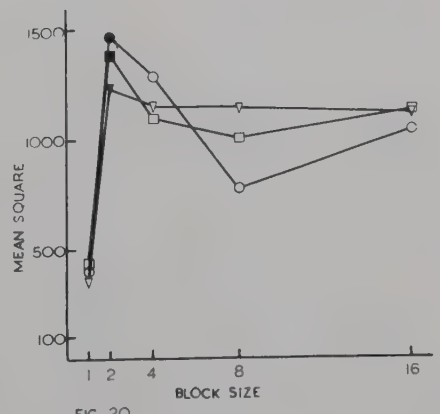


FIG. 20

●■▼ SIGNIFICANT PEAKS
○ 8 TRANSECTS
□ 16 TRANSECTS
▽ 32 TRANSECTS

FIG. 15-20. Mean square plotted against block size for cover data.

FIG. 15. 15% layout.
FIG. 16. 20% layout.
FIG. 17. 5% layout using a reduced basic unit.
FIG. 18. 10% layout using a reduced basic unit.
FIG. 19. 15% layout using a reduced basic unit.
FIG. 20. 20% layout using a reduced basic unit.

of the peak with an increase of mean square to $N_s = 4$ (Fig. 17). Consideration of the results from the 10% layout show a similar series of peaks with considerable evidence of drift to the right (Fig. 18).

This may be explained simply on the sampling procedure. The analysis is not sensitive to any overlap of basic unit with clump width when a small sample is taken from a community of low percentage cover. A large sample does detect this overlap effect (32 transects in Fig. 17) and in the 10% layout it is demonstrated by all sample sizes. This inaccuracy, due to inadequate sampling, is cancelled out in the 15% and 20% layouts, the increase of percentage cover to a 15% level being sufficient for even a small sample to eliminate most of the overlap effect, and in the 20% layout a clear peak at $N_s = 2$ is obtained (Figs. 19 and 20).

These experiments show the need for caution when the percentage cover of any species is in the region of 5%, and in such a case it may be necessary to sample that species separately with a basic unit of optimum size.

Field Trial

Since field data had not before been used in an analysis of this nature, a *Nardus-Calluna* community was selected in which the individual clumps of *Nardus* were distinct and readily measurable entities: 100 measurements of the clumps gave a mean diameter of 17.35 cms. (S.E.M. 5.39 cms.). Eight parallel transects were taken from the area, with cover readings taken every 1 cm. along their length. Individual readings were grouped into basic units of 5 cms., each unit being the observed cover expressed as a percentage of the possible total of 5; a single transect contained 128 such units. The percentage cover of *Nardus* was 18.22%.

There are two sharply defined peaks (Fig. 21) one at $N_s = 4$ corresponding to the mean measurement of the clumps taken by hand (1 unit 5 cms.) and one at $N_s = 32$. The larger scale heterogeneity was not apparent on a visual examination and it is probably a mosaic density effect. It is interesting to note that both peaks are significant using a classical F-test, the primary peak at the 0.1% level and the secondary peak between 1% and 5%.

Discussion

The mean dimensions of the scale of heterogeneity is shown by a peak in the curve mean square/block size, the sharpness of this peak being dependent both on the size of basic unit relative

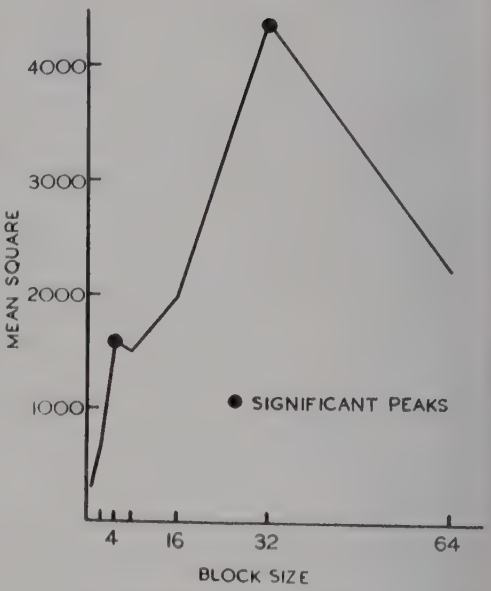


Fig. 21. Mean square plotted against block size for cover data of *Nardus stricta*.

to the size of "clump," and also to the size of the sample taken. The examination of any area of vegetation thus necessitates adequate sampling, the size of basic unit used being the first consideration:

Pattern in vegetation may be at several scales: a very small scale pattern due to the actual size of the individual, a secondary scale possibly due to the morphology of the individual, and one (or more) larger scales of pattern due to physiographic or sociological reasons. The first possible scale of pattern (the size of the individual) is a pattern to be expected and of academic interest only, but it does in any community fix the maximum size of basic unit that may be used to give optimum detection of the other larger scales of pattern. Thus if the individual is a large shrub then a large basic unit may be used, conversely if the species under investigation is a grass then the basic unit must be reduced to the smallest workable dimensions possible. It is in this respect that cover is the more suitable technique for work on grassland communities especially where the vegetation is of any great height. In such vegetation there is a practical limit below which the reduction of the size of a grid unit is not feasible; cover does not suffer these limitations, the basic unit being readily reduced to very small dimensions. The field data for *Nardus* (see above) using a 5 c.m. basic unit is entirely satisfactory,

and extensive further work on grassland communities has shown this basic unit to be an optimum size necessary for the adequate sampling of all scales of heterogeneity.

The considerations involved in determining the necessary size of sample to give an adequate analysis of any given area of vegetation, are not as straightforward. The necessary sample size may vary for different species within an area as well as varying from area to area, a situation commonly met with in any investigation involving a sampling technique. The usual approach to the problem is to increase consistently the sample size, plotting the fluctuations of the mean each time the sample is increased. When the mean has reached a stable level, a further increase in sample size is unnecessary. Similar considerations apply to the technique under consideration. The accurate detection of smaller scale pattern is assured if any apparent large scale pattern from a sample is persistently present in further samples taken. The "sharpness" of the peak may also be a good indication of the sufficiency of the sample, a gradual successive increase of mean square to a "peak" being an indication of the need for a larger sample.

To evaluate a contiguous grid involves a considerable amount of time and labour if the grid is larger than 256 units, whereas the possible sample sizes using cover as a measure are not limited to a geometric series. Similarly frequency data may also be obtained from a series of transects of contiguous units, a sampling procedure which may save considerable time in the field.

The subjective estimation of significance has proved to be remarkably reliable. Results using the cover technique (to be published later) show consistent peaking from area to area for all species considered, the pattern exhibited being due to morphological considerations or to sociological and physiographic reasons. Furthermore, it has been realized that the use of a classical variance ratio test is of value in deciding the true position of any peak despite the theoretical objections to its use, and in the majority of cases the subjective assessment of a peak is supplemented by a significant variance ratio test betwen the two adjacent block sizes.

Summary

A method using frequency and cover data to determine the dimensions of heterogeneity in plant communities is outlined. Adjacent transect readings are grouped together into different block sizes, the variance of any block size rising to a peak at the mean dimension of an area of heterogeneity.

The difficulty of testing the significance level of such a peak, once non-randomness has been established, is discussed, and, from the analyses of a series of experiments with artificial communities, a subjective approach to this problem is proposed. The experiments indicate the importance of using an optimum sample size and sampling unit, for the accurate detection of small scale pattern. A series of sampling experiments give an indication of the sample size required for a given level of percentage cover and it is suggested that the sampling unit be less than one half the size of the smallest dimension of an area of heterogeneity likely to be encountered in any given community.

Field trials on a *Nardus stricta* community indicate the accuracy of the technique, the actual dimension of the *Nardus* clumps being 17.35 cms. and the dimension given by the analysis, 20 cms.

Further field work has established that the final subjective approach to the significance of any apparent peak is reasonably sound, though it is suggested that a classical variance ratio test between adjacent block size values has a definite value in determining the true position of any peak.

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EARLY PLANT SUCCESSION ON ABANDONED CROPLAND IN THE CENTRAL BASIN OF TENNESSEE[1]

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The middle portion of Tennessee includes two physiographic regions, the Central or Nashville Basin, a large low calcareous area that is 60 miles wide and 120 miles long, with an average elevation of 600 feet (Fenneman 1938), and the surrounding Highland Rim that is 400 to 600 feet higher than the Basin. Both Rim and Basin lie within the Western Mesophytic Forest Region of Braun (1950), which is not a climax forest region but a transition zone between the Mixed Mesophytic and the Oak-Hickory Climaxes.

The lowest part of the Basin floor, where Lebanon limestone is exposed or thinly covered with soil, supports cedar glade vegetation that is quite distinct (Quarterman 1950) from that of the surrounding and interjacent uplands and rounded hills that comprise the rest of the Basin floor. High hills in the Basin that are outliers of the Highland Rim support plant communities characteristic of Rim vegetation (Braun 1950). For the intermediate slopes, Braun (1950) lists sugar maple as the chief tree in the original forests, with *Celtis laevigata, Ulmus americana, U. alata, Juglans nigra, Quercus borealis* var. *maxima, Q. Muhlenbergii, Q. macrocarpa, Carya ovata, Nyssa sylvatica, Prunus serotina,* and *Liquidambar Styraciflua* as accessory species. Cultivated land is usually on these lower slopes or on bottom land. Flood-plain cropland in the Basin is rarely abandoned and those fields on the uplands that are removed from cultivation are usually converted to pasture. This latter fact, unfortunately, made it impossible to locate more than a few fields of any given age over one year.

METHODS

Fields were selected from the intermediate slopes of the Basin, those on cedar glades, hilltops and flood-plains of major streams being excluded. The history of each field was ascertained in so far as possible, and only those whose histories included no grazing, mowing or burning were included. The fields sampled were all in the northwest quarter of the Basin, but fields in other parts of the area were examined, histories determined, and comparisons made with those where sampling was done. The same general pattern of succession appears to hold true throughout the Basin.

Sampling was done by the nested quadrat method, using plots ¼ by 1 m. in size for the herb layer, ½ by 2 m. for the woody seedling and shrub layer, and 2 by 8 m. for the tree size. Ten quadrats were counted in each field except for one first-year field whose species-area curve indicated such a small margin of safety that two more were added in this instance. Quadrats were regularly spaced, the distance apart varying from 5 to 20 paces depending on the size of the field. Data were kept separately for woody seedlings (under 1 ft. tall) and transgressives (1 to 10 ft. tall). Woody plants over 10 feet tall or over 1 inch d. b. h. were considered to be trees. Cover of herbs and shrubs was estimated and d. b. h. of trees measured.

For each species in each age field, frequency, density (average number of individuals per unit area), constancy, and cover (estimated) or basal area were determined. A summary figure (DFD index) was obtained for each species in each size class of every age field by adding relative frequency (Curtis and McIntosh 1950), per cent total density, and per cent total cover or basal area. Tables and diagrams were based on these summary figures.

Nomenclature follows that of Gray's Manual, 8th edition (Fernald 1950), except in quoting lists from the literature, when the nomenclature used in the publication is copied unchanged.

RESULTS

Twelve first-year fields were studied, 11 of which had been planted to corn the preceding year and 1 to okra. Sixty-four herbaceous species occurred in these fields but only 3 (4.6% of the total number), *Erigeron strigosus, E. canadensis,* and *Ambrosia artemisiifolia* var. *elatior,* had a constancy of 100%. They were also among the top 5 species by DFD index (Table I) and so are considered to be the chief dominants in this age field; however, *Aster pilosus, Gnaphalium obtusifolium* and *Ambrosia trifida* were each co-dominant with one or more of the major dominants listed above in at least one first-year field. The various combinations that may occur of two or more of these 6 species make possible the great

[1] This research was supported in part by funds made available jointly by the Carnegie Foundation and Vanderbilt University. The author is solely responsible for the statements made in this report.

TABLE I. DFD index of herbaceous species in fields of various ages. Species are arranged in descending order of importance according to the age field in which they first appeared. All herbaceous species included in sample plots are listed except for the following, whose DFD index was less than 1: in 1-year fields, *Artemisia* sp., *Cerastium* sp., *Diodia virginica, Draba* sp., *Hypericum punctatum, Melilotus alba, Opuntia humifusa, Plantago virginica, Sedum pulchellum, Setaria glauca, Specularia perfoliata, Trifolium pratense, T. procumbens,* unknowns; in 3-year fields, unknowns. x—present with less than 1 DFD; ?— present with less than 1 DFD, of the same genus but of undetermined species

Species	Age of field in years						
	1	2	3	4-8	12	15-20	25
Erigeron strigosus	50	27	1	x		5	..
Ambrosia artemisiifolia var. *elatior*	36	34	3	2	..	3	..
grass seedlings	33	..	1	5	36	..	38
Lespedeza spp.	29	37	13	23	.	37	
Erigeron canadensis	22	24	x	5			
Digitaria sanguinalis	20	138					
Aster pilosus	19	8	31	50	25	32	
Sida spinosa	13	11	2	3	16		..
Oxalis stricta	8	23	5	8			7
Cynodon dactylon	7	16					
Acalypha virginica	4		x	.	..	19	8
Physalis heterophylla	4	1	5				
Polygonum pensylvanicum	4						
Gnaphalium obtusifolium	3.9	14		6		2	
Solidago altissima	3.7	1	33	9	102	36	5
Cyrsium discolor	3			x			
Juncus dichotomus	3	11					
Verbena simplex	3	8					
Oenothera biennis	2.7						
Bromus japonicus	2.5	1	53	2			
Allium sp.	2.4	20	2	1	31		
Ipomea hederacea	2.4	6	3				
Euphorbia sp.	2.3	6					
Andropogon virginicus	2	18	11	97	13	11	
Diodia teres	2	10		x			
Xanthium sp.	2		x				
Ambrosia trifida	1.5		x				
Eupatorium serotinum	1.4	11					
Ranunculus abortivus	1.4						
Desmodium paniculatum	1.3						
Solanum carolinense	1.3	9	x				
Torilis japonicus	1.3	21	x				
Oenothera laciniata	1.2	6					
Lactuca scariola	1.1	1	2	x			5
Phyla lanceolata	1.1						
Plantago aristata	1.1	8					
Trifolium repens	1.1						
Euphorbia Preslii	1.08						
Verbascum Blattaria	1.06						
Daucus carota	1.03						
Verbascum Thapsus	1.03						
Chrysanthemum leucanthemum var. *pinnatifidum*	x			13			
Elymus sp.	x			x		18	
Capsella bursa-pastoris	x			x			
Chenopodium sp.	x	1					
Croton monanthogynus	x		x		7		
Gnaphalium purpureum	x	3		2			
Panicum sp.	x	..	..	1	..	..	81
Paspalum laeve var. *pilosum*	..	13	..	10			
Lepidium virginicum		8					
Cyperus sp.		3					
Panicum capillare		3					
Hypochaeris sp.		1		1			
Sorgum halapense		1			2		
Stellaria media		1					
Chaerophyllum spp.	..	..	28	..	14		

TABLE I. Continued

Species	Age of field in years						
	1	2	3	4-8	12	15-20	25
Geranium sp.	..	..	5	..			
Hieracium sp.	..	..	4				
Hypericum perforatum	..	..	2				
Eragrostis sp.	..	..	..	20			
Setaria geniculata	..	..	..	4	..	..	
Trifolium sp.	..	..	..	1	..	1	
Plantago lanceolata	..	..	..	1			
Achillea Millefolium	..	..	..	x	..	2	
Taraxacum officinale	..	..	..	..	7		
Triodia flava	..	..	..	..	..	11	
Carex sp.	..	..	..	..	..	4	
Melica mutica	..	..	..	..	..	1	
Sanicula marilandica	..	..	..	..	..	..	33
Geum canadense	..	..	..	..	..	..	32
Viola sp.	..	..	..	..	..	..	17
Galium sp.	..	..	..	..	..	..	13
Eupatorium coelestinum	..	..	..	..	..	..	13
Ranunculus sp.	..	..	..	..	..	..	9
Campanula americana	..	..	..	..	..	..	8
Desmodium sp.	..	..	..	..	..	..	6
Tragia cordata	..	..	..	..	..	..	2
Asplenium platyneuron	..	..	..	..	..	..	1

diversity in aspect that occurs in first-year fields. Of the possible major dominants, *Erigeron strigosus* is the only one that reaches its maximum growth and blooms in the early summer (Fig. 1), becoming less conspicuous as the other tall dominants become more conspicuous during the late summer and fall. *Lespedeza* spp. (*L. striata* and *L. stipulacea*) may occupy a sub-dominant position.

FIG. 1. First-year field during June. Note abundance of *Erigeron strigosus* throughout and scattered stalks of *Erigeron canadensis* in the foreground.

While 4 genera of tree seedlings were present, *Ulmus* (*U. serotina, U. fulva, U. alata, U. americana*) was the most important (Table IV). *Platanus occidentalis* and *Celtis* (*C. laevigata* and *C. occidentalis*) occupied second and third places respectively, but since *Platanus* occurred in only one first-year field and failed to show up in the counts of older fields, it may be considered an

FIG. 2. Second-year field during June, with a general mixture of species, including *Ambrosia, Erigeron canadensis* and *E. strigosus.*

accidental. *Symphoricarpus orbiculatus,* buckbush, was the only shrub present but several vines, chiefly *Campsis radicans* and *Cocculus carolinus,* were frequently abundant (Table V).

Two second-year fields (Fig. 2) were quite similar floristically, 44% of the total of 36 herbaceous species appearing in both fields. *Ambrosia artemisiifolia* var. *elatior* (DFD 34) was the only species with both constancy and frequency of 100%, but *Erigeron strigosus* (DFD 27) and *E. canadensis* (DFD 24) were important enough to consider them co-dominant in this age field (Table I). These 3 tall weed co-dominants were accompanied by *Diodia teres* (DFD 40), *Lespedeza striata* (DFD 37), and either *Digitaria sanguinalis* (DFD 130) or *Setaria glauca* (DFD 24) as subdominants. *Digitaria* formed an exceedingly dense (69% of total density) ground cover in one field; *Setaria,* although not so abundant (8% of total density), occupied a similar position in the other.

Andropogon virginicus, which had a DFD index of 2 in first-year fields, had increased to a DFD index of 18 in second-year fields.

Ulmus and *Celtis* were again the chief woody seedlings, *Juniperus virginiana* being the only other tree species present (Table IV). *Campsis radicans* was an important woody vine, as it had been in first-year fields.

Two third-year fields included a total of 36 herbaceous species, 27% of which were common to both fields. One of these fields was dominated by *Torilis japonicus, Aster pilosus* and *Solidago altissima,* while the other was dominated by *Solidago altissima, Aster pilosus* and *Chaerophyllum* spp. (*C. tainturieri* and *C. procumbens*), with *Bromus japonicus* as a subdominant. The two species with a constancy of 100%, *Aster pilosus* (DFD 31) and *Solidago altissima* (DFD 33), may be considered the nucleus of a group of dominants normally consisting of *Aster* and *Solidago* and one or more additional tall weeds and grasses (Table I).

In the third-year fields, the earlier dominants, *Erigeron strigosus, E. canadensis,* and *Ambrosia artemisiifolia* var. *elatior,* had dropped to negligible positions (Table I), but *Andropogon virginicus* showed no gain in importance over the second-year fields.

The *Solidago-Aster-Chaerophyllum* dominated field had been counted during its first year, at which time it was dominated by *Erigeron canadensis* (DFD 103.8), *Gnaphalium obtusifolium* (DFD 101), and *Aster pilosus* (DFD 88.1). In the first year, *Solidago altissima* (DFD 31.8) and *Bromus japonicus* (DFD 30.6) were present to a moderate degree, but no *Chaerophyllum* or *Andropogon* were included in the counts (Table II). By the third year, *Erigeron canadensis* and *Gnaphalium obtusifolium* had entirely disappeared, *Solidago* (DFD 110) and *Bromus* (DFD 226.5) increased in importance to dominant and subdominant respectively, and *Chaerophyllum* had invaded and become important (DFD 181.3). *Andropogon* had also invaded and become important (DFD 85.2). Of 23 species present the first year, 15 had disappeared leaving 8 still present; 6 new species had been added (Table II).

In third-year fields, *Ulmus* was the most important woody component, being present in both seedling and trangressive layers (Table IV). *Celtis* seedlings were present but there were none in the transgressive layers. In addition to these, *Quercus* spp. (*Q. prinus; Q. Muhlenbergii*), *Cercis canadensis* and *Fraxinus* seedlings were present. *Campsis radicans* was still very abundant.

Two fields who ages lay between 4 and 8 years were more consistent in their dominants than any fields of earlier ages, but had fewer species (13%) in common. *Andropogon virginicus* (DFD 97) and *Aster pilosus* (DFD 50) dominated both fields (Fig. 3), with *Solidago altissima* (DFD 9) present in both but of lesser importance. Total number of species had decreased from 36 in three-year fields to 30. One five-year field included only 7 species, 5 of which were held over from earlier years. This field had been counted during its second year of abandonment and at that time included 24 species, of which *Ambrosia artemisiifolia* var. *elatior* (DFD 111), *Diodia teres* (DFD 154.4) and *Digitaria sanguinalis* (DFD 456) were dominant, *Andropogon virginicus* (DFD 60.8), *Erigeron strigosus* (DFD 62.5), *E. canadensis* (DFD 50.8) and *Eupatorium serotinum* (DFD 76) were moderately important, and *Aster pilosus*

TABLE II. Relative importance (DFD) of herbaceous species in the same field 1 and 3 years after abandonment

Species	Age of field in years	
	1	3
Erigeron canadensis	103.8	.....
Gnaphalium obtusifolium	101.0	.....
Aster pilosus	88.1	88.9
Oxalis stricta	70.5	41.1
Sida spinosa	67.8	31.0
Ambrosia artemisiifolia var. *elatior*	51.3	.....
Lespedeza striata	50.8	21.5
grass seedlings	34.1	.....
Polygonum pensylvanicum	33.8	.....
Solidago altissima	31.8	110.0
Bromus japonicus	30.6	226.5
Acalypha virginica	21.4	.....
Solanum carolinense	20.4	10.1
Erigeron strigosus	10.4	10.3
Cirsium sp.	10.2	.....
Desmodium paniculatum	10.1	.....
Draba sp.	10.1	.....
Elymus sp.	10.1	.....
Euphorbia sp.	10.1	.....
Lactuca scariola	10.1	.....
Oenothera laciniata	10.1	.....
Physalis heterophylla	10.1	.....
Torilis japonica	10.1	.....
Chaerophyllum sp.	.....	181.3
Andropogon virginicus	.....	85.2
Geranium sp.	.....	62.7
Hieracium sp.	.....	44.0
Ipomea sp.	.....	40.6
Allium sp.	.....	30.7
Total number of species	23	14

(DFD 30.7) present (Table III). Of this group, *Aster* (DFD 123.6) and *Andropogon* (DFD 126.2) had increased enormously in frequency and density by the fifth year, *Ambrosia* was present but negligible (DFD 10.7), and the others failed to appear in the counts. *Solidago altissima* (DFD 11.2) and *Panicum* sp. had been added in the three-year interval (Table III).

The only woody seedlings present were *Ulmus* and *Celtis,* but these genera were not represented

FIG. 3. Four-to-eight-year field dominated by *Andropogon* and *Solidago.* Photographed in September.

FIG. 4. Field between 15 and 20 years of age. Note elm in the foreground.

TABLE III. Relative importance (DFD) of herbaceous species in the same field 2 and 5 years after abandonment

Species	Age of field in years	
	2	5
Digitaria sanguinalis	456.0	.....
Diodia teres	154.4	.....
Ambrosia artemisiifolia var. *elatior*	111.0	10.7
Solanum carolinense	81.2	.....
Eupatorium serotinum	76.0	.....
Sida spinosa	72.1	30.6
Allium sp.	72.0	.....
Lespedeza sp.	71.5	.....
Erigeron strigosus	62.5	.....
Andropogon virginicus	60.8	126.2
Juncus sp.	52.2	.....
Verbena simplex	51.2	.....
Erigeron canadensis	50.6	.....
Euphorbia sp.	40.8	.....
Gnaphalium obtusifolium	40.5	.....
Oxalis stricta	40.4	.....
Aster pilosus	30.7	123.6
grass seedlings	20.4	10.1
Ipomea sp.	10.3	.....
Cyperus sp.	10.1	.....
Physalis heterophylla	10.1	.....
Plantago aristata	10.1	.....
Solidago altissima	.....	11.2
Panicum sp.	.....	10.1
Total number of species	22	7

in the transgressive layer; transgressives of *Maclura pomifera* were fairly important. *Cocculus carolinus* occurred in addition to *Campsis;* from this age onward, *Campsis radicans* diminished in importance (Table V).

One field in the twelve-year age class was counted. Its history differed from that of other fields in that during its last year of cultivation a bulldozer had been used in making terraces, which disturbed the topsoil more than ordinary cultivation would have done. This field was dominated by *Solidago altissima* (DFD 102), *Andropogon virginicus* (DFD 43) in widely scattered clumps,

Aster pilosus (DFD 25) and a ground cover of unrecognized grasses.

Symphoricarpus orbiculatus formed large thickets that dominated the transgressive layer (Table V). *Rubus* sp. also occurred with a considerable degree of regularity. The importance of *Maclura pomifera* and of *Cercis canadensis* is exaggerated in Table IV because no other species occurred in the tree size class. (This illustrates a certain lack of accuracy in the use of the importance index where a few figures produce high percentages for each species involved. Actually, *Cercis* had a frequency of 10 and an average density of 0.4, or a total of 4 individuals all located in one plot.) Both *Ulmus* and *Celtis* occurred in the seedling layer and *Ulmus* in the transgressive layer (Table IV).

A 15-20-year field had the aspect of very open woods (Fig. 4) with the herb layer dominated by a combination of *Solidago altissima* (DFD 36), *Aster pilosus* (DFD 32), *Andropogon virginicus* (DFD 41), and *Panicum* sp. (DFD 81). *Symphoricarpus* and *Rubus* occurred in widely spaced thickets. *Ulmus* and *Celtis* were represented in the seedling, transgressive and tree layers (Table IV), dominating the present stand and indicating probable continued dominance as seedlings and transgressives mature. *Juniperus virginiana* and *Cercis canadensis* occurred in the seedling and tree layers, *Fraxinus americana* in the transgressive layer and *Crataegus* sp. in the tree layer.

The 25-year stand was a young woods with a few open spaces in it. The tree layer, not yet old enough to be differentiated into over-and understory, consisted largely of *Ulmus* and *Celtis* (Fig. 5), but also included *Quercus Muhlenbergii, Asimina triloba, Acer saccharum, Diospyros virginiana, Gleditsia triacanthos, Juglans nigra, Morus rubra* and *Quercus rubra*.

Celtis, Ulmus, Symphoricarpus, Asimina, Morus and *Quercus rubra* made up the counted transgressive layer, but *Q. Muhlenbergii* was observed in this stand outside the quadrats.

Seedlings of *Ulmus, Celtis, Asimina, Bumelia* and *Nyssa sylvatica* were present, *Ulmus* seedlings having the greatest relative importance (Table IV).

The herb layer of the 25-year old stand was composed of 15 species, most of them different from those of the younger stands. The shift in herbaceous species evidently occurs as the crown cover closes over, because the remnants of open field species occurred in the spaces between the trees. A combination of *Sanicula trifoliata, Geum virginianum* and unknown grasses dominated the herb layer (Table I).

FIG. 5. Interior of a 25-year stand. The forest canopy here is nearly closed. Hackberry (center) and elm (foreground) are major dominants of this stand.

DISCUSSION

While Table I illustrates the lack of distinctiveness of herbaceous stages and the number of co-dominants that may occur, especially in the first few years, Figure 6 shows certain components that link two or more stages together. Each species whose relative importance is plotted here was a dominant through two or more stages. In reporting such a line of continuity, one necessarily over-simplifies, so it is important to remember the abundance of co-dominants (Table I) in most of these stages. The early dominants, *Erigeron* spp. and *Ambrosia*, decline in importance rapidly after the second year, although they may occasionally be found in much older fields. All three dominants of later years, *Aster, Solidago*, and *Andropogon*, occurred in first-year fields. *Andropogon* and *Aster* reached their greatest peak in the 4-8-year fields, *Solidago* in the 12-year field. The latter three species were of nearly equal importance in

TABLE IV. DFD index of woody species by size class in different aged fields. Species of *Ulmus* (*U. alata, U. americana, U. rubra, U. serotina*), *Celtis* (*C. laevigata, C. occidentalis*) and *Quercus* (*Q. Muhlenbergii, Q. prinus*) could not be distinguished from each other as seedlings, so these species are grouped together. s—seedlings; ts—transgressives; tr—trees

Species	Age of Field in Years																					
	1			2			3			4-8			12			15-20			25		
	s	ts	tr	s	ts	tr	s	ts	tr	s	ts	tr	s	ts	tr	s	ts	tr	s	ts	tr
Acer negundo	2.1																				
Celtis spp.	9			45			14.7			30			4.6			27	28	116	3.7	5.7	109
Juniperus virginiana	2.2			18												9		26			
Platanus occidentalis	14.5																				
Prunus serotina	2.1																				
Ulmus spp.	43	3.5		47			5	10		80			7	17		31	20	66	13	10	53
Cercis canadensis				10.7											50	4	40				
Fraxinus americana				4.5													4	24		2.2	
Quercus spp.				15.8																	5.7
Maclura pomifera											12			4.6	150					20.0	
Crataegus sp.																		27			
Acer saccharum																					4.7
Asimina triloba																			2.5	2.2	10
Diospyros virginiana																					5
Gleditsia triacanthos																					12
Juglans nigra																					38
Morus rubra																				2.2	22
Nyssa sylvatica																			2.2		
Quercus rubra																				2.2	5

TABLE V. DFD of shrubs and woody vines by size class in different aged fields. u—under 1 ft. tall; o—over 1 ft. tall

Species	Age of Field in Years																					
	1			2			3			4-8			12			15-20			25		
	U		O	U		O	U		O	U		O	U		O	U		O	U		O
Bignonia capreolata	2.1															9					
Campsis radicans	114			83			6.2								12			11			4
Cocculus carolinus	80														9			45			23
Passiflora incarnata	4.6									53											
Rubus spp.	11						6.2								67						
Symphoricarpus orbiculatus	2.1						125						4.6		173			30	6		22
Rhus toxicodendron												12									
Rhus radicans																8			78		
Rosa spp.																9					2.2
Rumelia lycioides																			2.2		
Clematis virginiana																			2.2		
Parthenocissus quinquefolia																			3.9	5	
Vitis sp.																				5.7	

the 15-20-year field, but only *Solidago* occurred in the counts in the 25-year field.

The data obtained by recounting two fields within the 1-5-year interval increase the author's assurance that the shift in dominance as age increases is real and not occasioned by the chance finding of possibly abnormal fields (Table II). The marked changes that occurred between countings in these fields are in agreement with the general trend of events determined by inference from the quadrat studies of fields of various ages.

Drew (1942) has pointed out the remarkable floristic similarity of early dominants of old fields throughout a given climax region, and the Middle Tennessee fields are no exception. They fit into a general floristic scheme in similar secondary successions in the Eastern Deciduous Forest Region; however, quantitative studies of secondary succession in abandoned fields indicate certain differences in community structure in different parts of the climax region. A comparison of dominants as reported by Bard (1952) for the transition from Oak-Hickory to Hemlock-Hardwoods on the glaciated Piedmont of New Jersey, by Oosting (1942) for the Oak-Hickory of the Atlantic Piedmont in North Carolina, by Drew

(1942) for the transition to Prairie from the southern division of the Western Oak-Hickory Forest in Central Missouri, and this report from the Western Mesophytic Forest Region shows some notable dissimilarities as well as many similarities. These three papers were selected for especial emphasis because each deals with a different association of the Eastern Deciduous Forest, and each is in some way comparable to the present study. In addition to these papers and those summarized by Drew (1942), other more recent reports of old field studies (Bonck and Penfound 1945; Marks 1942; Warner and Aikman 1943; Kurz 1944; Warner 1945; Cain and Evans 1952; Evans and Cain 1952; Niering 1953) were considered. Since no comparisons of these with Middle Tennessee data are to be drawn here, discussion of them seems superfluous.

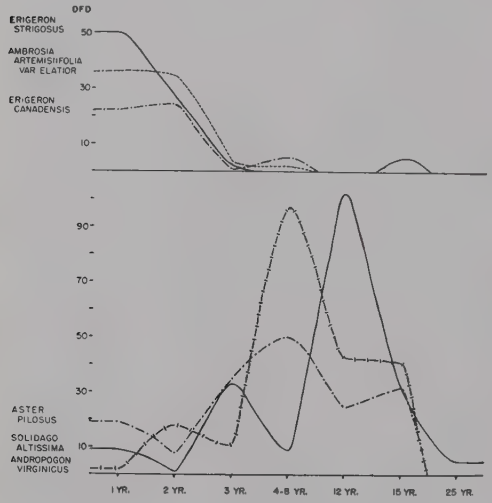

FIG. 6. DFD index of dominant herbaceous species plotted against age of fields. Data from twelve 1-year, two 2-year, two 3-year, two 4-8-year, one 15-year and one 25-year field.

The early summer dominance of *Erigeron strigosus* during the first year of abandonment in Middle Tennessee is a conspicuous feature that is not reported from other areas. Bard (1952) records it from all age fields through 60 years, but its importance is minor. Drew lists it for second-year and third-year fields and occasionally thereafter up to 30 to 35-year fields; the highest frequency reported for it was in the 3-year fields, when it attained a frequency of 55% and a density of 8.4 (Drew 1942). Oosting does not list it for any of the fields in which herbs were counted, but mentions its abundance in pastured fields. It occurs in Middle Tennessee in pastured fields that are four years of age or over. McQuilkin (1940), in reporting the place of pines in revegetation of old fields in the upper Piedmont of North Carolina, South Carolina and Virginia, calls *Erigeron ramosus* (*E. strigosus*) a subdominant in early stages of succession; in Tennessee, it is more important than its co-dominants, *Erigeron canadensis* and *Ambrosia artemisiifolia* var. *elatior*. It is mentioned by Warner (1945) as occurring in Central Iowa on "shallow, eroded soils of high acidity"; in Tennessee, it occurs on good soils rather than in eroded fields. Its restriction to the better soils is quite noticeable where erosion is severe in certain portions of a given field.

In no other area is *Erigeron strigosus* reported to occupy a position of primary importance in early old field succession. It occurs, however, throughout most of the Eastern Deciduous Forest Region, and so one wonders why it becomes a dominant in the Central Basin of Tennessee and not elsewhere in its range. Its life cycle corresponds fairly well during the early stages with that of *E. canadensis*, horseweed, whose seeds germinate in the fall, whose seedlings over-winter as rosettes and grow to maturity the following year (Keever 1950). *Erigeron strigosus*, a long-day plant, matures in June; it is possible, therefore, that its seedlings become established somewhat earlier than those of horseweed, that matures in early fall. If seedlings of both are established during late summer and early fall, it seems that competition between the two would be keen and that one or the other might be eliminated or subordinated at that time. Instead, one follows the other as its time of maturity occurs (Fig. 1), each assuming an aspect dominance in its season. Why does this happen in Tennessee and not in North Carolina, also? There are several possible explanations. One, that there are enough nutrients and water available in the Central Basin to eliminate competition, seems most unlikely. Wider spacing of plants in the fields would have such an effect, but the data are not comparable on this point. Another possibility is that there is an increase in the vigor of *E. strigosus* or a decrease in the vigor of *E. canadensis* in the Basin as compared with the Piedmont. *E. strigosus* introgresses with *E. annuus* in parts of the eastern United States (Anderson 1949). Since both species occur here, a careful taxonomic study of the old field erigerons is desirable to see if the difference in ecological position of *E. strigosus* might be explained by the presence of intraspecific genotypes, possibly originating from introgression.

In the fall, the resemblance of the old fields in

the Central Basin to similar-aged fields in the Piedmont is striking. *Erigeron strigosus* in many fields is being overtopped by *E. canadensis* that is often the conspicuous dominant of late summer and fall. While *Erigeron* spp. and *Ambrosia* are usually among the first-year dominants, the fact that they may share dominance with one or more other tall herbs makes for a less clear-cut first-year stage than occurs in North Carolina (Oosting 1942). This distinct year by year shift of unmistakable dominants during the first few years appears to be the exception rather than the rule. Braun (1950) relates the simplicity of old field succession to the periphery of the Deciduous Forest where the climax dominants are also few in number. She contrasts such areas with those in which Mixed Mesophytic Forest is climax and where "the early stages of subseres are legion."

The later stages in the study area differ markedly from those in North Carolina, where *Aster* is dominant during the second year and *Andropogon* from the third year until replaced by pines (Oosting 1942). They more nearly resemble the 2- to 5-year fields described by Bard (1952) even though the species differ. The gradual change to *Aster-Solidago-Andropogon* dominance, accompanied by the occurrence of many accessory species, seems to be similar, also, to the 2- to 5-year situation in Cedar Creek, Missouri (Drew 1942).

Keever (1950) concluded that the reasons for change of dominance in fields in North Carolina lie in timing of life cycles of horseweed and *Aster,* and in competition for light and water causing *Aster* to be replaced by *Andropogon.* The same species are important in early succession in Tennessee, but each shares dominance with one or more additional species, and the number of variables is thus multiplied. Of the possible first-year dominants, *Erigeron canadensis* and *E. strigosus* germinate in the late summer or fall and overwinter as rosettes, *Aster pilosus* germinates in the spring (Keever 1950), as do both the *Ambrosia* species. Nothing is known of the germination time of *Gnaphalium obtusifolium.* Why don't the same species fill the same niches in Middle Tennessee that they do in North Carolina since all are present in both areas?

The greater total number of individuals in Tennessee fields as compared with those in North Carolina may create enough competition to prevent horseweed from becoming the chief dominant, since it does poorly in competition with other plants (Keever 1950). The surviving horseweed plants are tall and vigorous, however, and do not compare in size with horseweeds of second-year Piedmont fields, where competition has been keen. The early light shade furnished by *Erigeron strigosus* might be of advantage in the establishment of some species, giving them a better chance to survive during the early part of the season, but this is not likely the case with horseweed.

Aster was never found as a single dominant except where regular mowing had occurred. Such areas were not sampled, but this indicates that competition may be a most important factor in preventing *Aster* from assuming complete dominance. *Aster* shares dominance in 3-year fields with *Solidago* and in 4- to 8-year fields with *Andropogon.* It seems odd that both *Aster* and *Andropogon* should increase in importance simultaneously in the same field (Table III) when Keever's (1950) work indicates that the competition between the two eliminates *Aster* from the North Carolina fields. Broomsedge fails to develop the complete cover in Tennessee that it does in North Carolina, and the wider spacing may leave room for *Aster* to develop normally. This answers one question, but poses another. Why doesn't broomsedge form a complete cover in the Tennessee fields?

Solidago shares dominance in 3-year fields with *Aster* and in 4-to-8-year fields with *Andropogon,* then becomes of greater importance than *Andropogon* by the twelfth year. Life history studies of *Solidago* are therefore desirable, in order to clarify its relationship to these co-dominants. Broomsedge starts to die out at about the twentieth year even where it is not shaded by trees, but *Solidago altissima* is still vigorous at that time. This is just the opposite situation to that in New Jersey (Bard 1952) where *Solidago nemoralis* loses dominance after the tenth year and *Andropogon scoparius* becomes completely dominant at that time.

No pure stands of broomsedge were found in the Central Basin except in abandoned pastures where grazing had apparently kept down the more palatable herbs and grasses. It is considered to be one of the worst of the pasture weeds.

The first woody dominants in Middle Tennessee fields differ from those so far reported in other old field successions. They are species of *Ulmus* and *Celtis,* as compared with pines in the southeastern Piedmont (Oosting 1942; McQuilkin 1940), with *Diospyros virginiana* and *Sassafras albidum* in Missouri (Drew 1942), and with *Juniperus virginana* in New Jersey (Bard 1952). No species of pine are native in Tennessee's Central Basin. *Diospyros* and *Sassafras* occur here in some abundance, however, and *Juniperus virginiana* is the only native evergreen and therefore very conspicuous. It is most abundant in cedar

glades, but also occurs on rocky hillsides and incidentally in any type of stand. Drew (1942) notes that sassafras and persimmon are unimportant in revegetation of fields except in the forest-tall-grass prairie ecotone. Elm and hackberry both occur there, too, yet their relative importance is far less. Dispersal of hackberry seed by birds and of elm by wind certainly give them an advantage in Middle Tennessee over sassafras and persimmon whose seeds are not widely scattered, but not over red cedar because the birds carry these seeds widely also. *Juniperus* occurs here in old pastures or grazed fields where its dominance is determined by grazing rather than by a "fire-free history" (Bard 1952) as in New Jersey. It may be of greater importance in ungrazed fields in cedar glade parts of the Basin but these were eliminated from the present study.

The floristic composition of the total list of woody species (Table IV) in the 22-year stand is remarkably similar to Braun's (1950) list of dominant species of the original forest on the intermediate slopes in the Central Basin. Two-thirds of the 12 species she listed are represented in this 25-year stand. Of the four not represented, *Prunus serotina* and *Liquidambar Styraciflua* are not important in existing mature stands in the Basin. This seems to indicate that the *Celtis-Ulmus* stage might immediately precede a mature woods similar to the original stands, since it is most unlikely that any one stand would include the entire list of significant species, especially in a transition zone where the mature stands that still exist vary so much floristically, even on apparently similar habitats. Perhaps the complexity of both herbaceous and forest stages is a reflection of the transitional nature of the region, where vegetation readily reflects slight differences in site and microclimate.

Any effort to determine the reasons why certain species occur in different ecological positions in different parts of a given climax region must depend on several lines of future research. These are, (1) autecological studies to determine the life cycles and requirements or tolerances of individual species that may throw light on the means by which they fit together into communities, (2) investigations into the variability of the species populations involved, to determine if strains within species may possess physiological characteristics that give them an advantage in certain habitats, and (3) studies leading to a better understanding of the influence of climatic, edaphic, and historical factors in determining the segregation of certain species into successional as well as climax communities. Before the entire picture of old field succession in the Eastern Deciduous Forest Region can be distinguished, more descriptive studies must be made, preferably using similar quantitative methods, the results of which can readily be compared. Until this is accomplished, our knowledge of the pattern will continue to resemble a jig-saw puzzle with many of the pieces missing, and the search for causes will lack the guidance that a more complete knowledge of the pattern would furnish.

Summary

Studies of plant succession in abandoned fields in the Central Basin of Tennessee were made, using the nested quadrat method of sampling. Fields varying in age from one to 25 years were sampled. The following sequence of dominants occurs: first year, *Erigeron strigosus, E. canadensis* and *Ambrosia artemisiifolia* var. *elatior;* second year, *Ambrosia artemisiifolia* var. *elatior, Erigeron strigosus, E. canadensis* and many incidental species; third year, *Aster pilosus, Solidago altissima, Bromus japonicus* and other tall weeds; fourth to eighth year, *Andropogon virginicus* and *Aster pilosus;* twelfth year, *Solidago altissima, Andropogon virginicus* and *Aster pilosus;* fifteenth year, open woods of *Ulmus* and *Celtis* with an herb layer dominated by *Andropogon virginicus, Solidago altissima, Aster pilosus* and *Panicum* sp.; twenty-fifth year, *Ulmus* and *Celtis,* with an herb layer composed chiefly of *Sanicula trifoliata, Geum virginianum* and grasses. Additional woody species in the 25-year old field suggest a definite trend toward the same composition as occurred in original stands on similar sites.

Several distinctive features may be emphasized, first, the obscuring of clear-cut dominance and shifts of dominance from year to year by the presence of many accessory species, second, the importance of *Erigeron strigosus* in first and second-year fields, and third, the occurrence of *Celtis* and *Ulmus* as first woody dominants, a position that they do not appear to assume elsewhere.

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AN EXPLORATORY STUDY ON SOIL ALGAE[1]

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INTRODUCTION

This study was undertaken to test methods and suggest plans to be used in a projected survey of soil algae in central Oklahoma. The primary questions were methods of sampling and treatment and evaluation of samples.

Certain prior decisions were made simply to delimit the study: the depth involved would not exceed the plow layer (7 inches); and the presence only, not numbers of algae would be recorded for an area. During the study, it was hoped to learn something about: a. vertical floral variability within the plow layer; b. the homogeneity of the algal flora within a soil area having a common origin of parent material and covering of native vegetation; c. the extent of variation through a season (spring); d. the effect of different collecting techniques; e. the effects of enriching soil-water cultures; f. the effect of two types of light.

Historical Survey

There are few precedents in methods and plans to be followed for an extensive survey of soil algae. Regional fresh water floras have included whatever soil algae appeared conspicuously on the surface, but it has not been customary to collect them systematically. At least two Oklahoma studies have included soil algae. Booth (1941) collected crusts, as did Vinyard (unpublished), but neither attempted culturing to develop inconspicuous flora.

An historical account of previous soil algae literature was prepared by Peterson (1935) in his writing on Danish soil algae, and studies have been published for Australia (Tchan and Whitehouse, 1953); India (Mitra, 1951); Roumania (Grintzesco, 1929); Germany and Scandinavia (Feher, 1936); and Canada (Lowe and Moyse, 1934). Among these, only the study by Feher which covered 30 stations betewen 46° and 70° north latitude, could be called a broad survey. Local studies only have been described for the United States.

Few ecological techniques or standards of expectancy were developed in the above studies, since their primary interest was elsewhere. Some English studies (James, 1935) (Lund, 1945, 1947), however, have dwelt considerably on procedure. Lund collected the top two centimeters of soil with a sterile knife, examined thin surface and subsurface slices, plated samples, cultured with Benecke solution (0.05%), and conducted quantitative plate counts. Following this procedure, he discussed seasonal succession, distribution, and microstratification in some detail.

[1] The aid of Wm. T. Penfound in planning the study and preparing the manuscript is gratefully acknowledged. E. L. Rice was most helpful during the planning phase, and Dr. Francis Drouet checked identifications of several of the algae.

A few additional guides to the conduct of a survey are available. It has been rather well established that the algal flora changes with depth, if only by a decrease in numbers. Moore and Carter (1926) and Smith (1944) are among those documenting this conclusion.

Finally, in a study of soil fungi of virgin prairie and adjacent cultivated plots in Oklahoma, a useful sampling technique was suggested. McElroy (1953) collected ten samples monthly in diagonal transect from plots, amalgamated them, and used the soil itself in petri plate cultures. That procedure was adapted to the present study, but the quantitative aspects of the fungus study were not followed.

Areas Studied

Two localities were sampled. The principal area was the University of Oklahoma Grassland Investigation Plots located eight miles southwest of Norman, Oklahoma, along State Highway Nine in McClain County. Studies are available for the area giving some detail of higher plant vegetation and soils (Kelting, 1951) and succession (Rice and Penfound, 1954). Collections were taken from protected prairie and cropland. The prairie has not been plowed, as far as is known, and had been only moderately grazed up until about 1949, ungrazed since. The cropland has been plowed yearly since 1949, and usually planted with a farm crop.

The other location was the C. L. Taylor farm located about fourteen miles east of the above area. It was a mile east, and one quarter mile north of the northern city limits of Noble in Cleveland County. This area was unplowed prairie, slightly overgrazed, similar, but not identical in soil type and cover to the other prairie.

Sampling

The areas actually sampled were about a half acre in size and appeared to be covered with a rather uniform mixture of flowering plants. Samples were removed at ten-pace intervals. 7 along a line parallel with the long axis of the plots and 3 perpendicular to the long axis.

Sampling dates were March 28, April 26, and May 28, 1956. From the protected pasture, 3 types of samples (10 each) were taken: a. surface—including litter and approximately one quarter inch of soil; b. auger—obtained with a one and one half inch soil auger which drilled to a depth of 6 to 6.75 inches; c. the Willson Core Collector—a 6 inch length of three quarter inch pipe was fitted with a T on the top. This pipe could be forced into the ground with the heel or pressure on a rod thrust horizontally through the T. The same rod was used to pull the apparatus from the ground, then to force the core out by pressure through a hole in the top of the T pipe. The cores were difficult to remove, hammer blows on the top of the rod being required, however, fairly solid cores were obtained in this way, as desired.

In the cropland plot, surface and auger samples (10 each) were mixed thoroughly. Cores were divided into top, middle, and bottom thirds.

From the mixed samples (surface or auger) teaspoon portions were placed in 15 petri dishes (20 in March). Fifteen plates of the core samples contained two each of top, bottom, or middle portions. The petri plate culture method of Warcup (1950) was generally followed, with filter paper placed at the bottoms in the manner used for soil crusts by Fletcher and Martin (1948).

Sterile cistern water was added to 5 of the 15 culture plates containing surface or auger amalgamations, and to one of the 5 containing top, middle, or bottom core samples. Mineral solution was added to 5 of the 15 surface and auger plates, 2 of the 5 core plates, and organic solution to an identical series. Sufficient liquid was used to cover the bottom of the dish but to leave some of the soil above its surface. The mineral solution used was Hoagland's #1 (Hoagland and Arnon, 1938) with minor element supplement, diluted to one quarter of the suggested concentration; the cistern water came from a galvanized iron gutter and pipe system, and organic solution was composed of .2% dextrose, .01% acetic acid, .02% peptone, about 0.2% yeast extract.

Twenty-four hour lighting was provided by fluorescent tubes. One of the light banks contained "white" tubes illuminating the plates at 60-201 foot-candles, the other was the "daylight" type and illuminated at 50-204 foot-candles. The variation was due to the position of different plates in relation to the light, but experience of algae culturists (e.g., Dr. Jack Myers, personal communication, March, 1956) has indicated that the results of this study were probably not altered thereby. The type of light was recorded for all plates, and parallel series were set up under the lights with surface and auger samples using prairie soil.

Observations and Results

A casual daily check was kept of the plates during the first two months; however, substantial growth occurred in about 1 or 2 weeks and a final examination was conducted 4 weeks after collection. Colonies in a plate were examined microscopically until it was judged that nothing new

TABLE I. Summation of identifications from all samples. Date: March (M), April (A), and May (M); Location: Po—experimental area prairie, Co—experimental area cultivated field, Pn—Noble prairie; level: S—surface, A—auger, C—core

	PoS MAM	PoA MAM	PoC MAM	CoS MAM	CoC MAM	PnS MAM	PnA MAM
Plectonema nostocorum Born.	x x x	x x x	x x x	x x x	x x x	x x x	x x x
Phormidium autumnale (Ag.) Gom.	x x x	x x x	x x x	x x	x x	x x x	x x x
Nostoc muscorum Ag.	x x	x x	x x x	x x	x x	x x	x x x
Cylindrospermum licheniforme (Bory) Kuetz.	x x	x x	x x	x x x	x x x	x x	x x
Nostoc ellipsosporum (Des.) Rab.	x x x	x	x x	x x	x x	x x	x x
Microcoleus rupicola (Tild.) Drou.	x x	x x		x x x	x x x	x x x	x x
Schizothrix Stricklandii Drou.	x x	x x	x x	x x x	x x	x x	x x
Chlamydomonas spp. 1	x x	x x	x x	x	x x	x x	x x
Lyngbya aestuarii (Mert.) Lieb.	x x x	x x	x	x x x		x x	x
Anabaena oscillarioides Bory	x x	x	x	x	x	x	x
Schizothrix lardacea (Cesati) Gom.	x	x		x x	x	x	x
Hantzschia virgata (Roper) Grun.	x x		x x	x		x	x
Navicula spp.	x x	x	x		x x		
Chlorococcum humicola (Naeg.) Rab.	x	x x	x	x			
Chlorococcoid organism		x	x x				x
Protosiphon botrycides (Kuetz.) Klebs.		x x					x
Scytonema Hofmannii Ag.				x		x	
Fremyella spp.			x				
Dactylococcopsis Smithii Chodat and Chodat			x				
Symploca muscorum (Ag.) Gom.					x		
Chlamydomonas, spp. 2					x		
Chlamydomonas, spp. 3			x				
Synedra ulna (Nitzsch) Ehr.	x						
Ulothrix flaccida Kuetz.	x						
Anisonema spp.	x						

was being encountered. The analysis was concerned only with presence or absence in the series of plates.

The identifications from collections for the entire season's study are summarized in Table I. It is quite apparent that the same common species were encountered in the three situations by the three different collecting methods and in the three months of the study. At most times identifications from an amalgamated collection from a single plot corresponded rather well with those of total collections for the entire study. A common spring flora is certainly indicated for the plow layer of the prairie soils of Central Oklahoma. Hence there is some justification for a survey to take samples every two or three months from areas based on higher plant vegetation and soil type.

Identifications from the core samples are summarized in detail in Table II. The same flora is indicated from top, middle, and bottom samples (approximately 0 to 2 inches, 2 to 4 inches, and 4 to 6 inches respectively). Except in the late May collection from the cultivated field, the number of species encountered decreased with depth. Even though no quantitative analysis was attempted, it was also obvious to the examiners that the number of colonies in the bottom core plates was markedly less than in the upper ones.

The results of two separate kinds of sample treatment are indicated in Table III: a. white and daylight tube illumination; and b. addition of 3 liquids to the soil—cistern water, mineral solution, and organic solution. The results are erratic, and probably reflect chance rather than any trend. The common species, at least, appeared under either light, in any liquid. However, it was obvious that colonies in mineral or organic solution

TABLE II. Comparison of species identified from six inch core samples. Top third (T); Middle (M); Bottom (B)

	PoC			CoC		
	T	M	B	T	M	B
P. nostocorum	23	123	23	1	123	13
P. autumnale	3	2	3	12	2	1
N. muscorum	123	3	3	1	3	13
C. licheniforme	2	12	1	12	12	13
N. ellipsosporum	1	12	12	12	1	..
M. rupicola	2	...	..	12	23	2
S. Stricklandii	...	...	..	23	...	23
Chlamydomonas, spp. 1	...	12	12	12	12	1
L. aestuarii	2	...	..	..	...	..
A. oscillarioides	1	...	1	..	1	3
S. lardacea	...	...	..	3	...	3
H. virgata	3	...	..	..	...	..
Navicula spp.	2	...	..	2	...	..
C. humicola	1	...	..	..	...	..
Chlorococcoid organism	2	1	..	..	...	..
Fremyella sp.	12	...	..	..	...	..
S. muscorum	...	...	..	2	...	..
Chlamydomonas, spp. 2	...	...	..	..	...	3
Total species March (1)	5	5	4	7	4	4
April (2)	8	4	3	7	5	2
May (3)	4	2	2	2	3	6

TABLE III. Identifications from soil-water cultures grown under white and daylight type fluorescent tubes, with and without enrichment of culture liquid. Pow—experimental area prairie, white, Pod—experimental area prairie, daylight, Cow—experimental area cultivated field, white, Cod—experimental area cultivated field, daylight, Pnd—Noble prairie, daylight; c—cistern water, m—mineral solution, o—organic solution; March (M), April (A), and May (M). Only the OU pasture cultures (A) are recorded in parallel lighting series. (*B*) and (*C*) show the same sort of patternless distributions. There was no April record for Cod

	A		*B*		*C*
	Pod MAM	Pow MAM	Cod MAM	Cow MAM	Pnd MAM
P. nostocorum	c c c m m m o o	c c c m m m o o o	c m m o o	c c c m m m o o o	c c c m o o
P. autumnale	c m o o	c m m o o o	o	c c m m o o	c c c m o o
N. muscorum	c m o	c c o o	c m m o	c c m m o	c o o
C. licheniforme	c m m	c c m o	m m	c c c m m m o o o	c c
N. ellipsosporum	c c o	c c c	c	c o o	c c m o
M. rupicola	c c m m o o	c c c m o o	m m	c c m m o o	c c
S. Stricklandii	o	m	c m m o o	c c m o	c c c m o o
Chlamydomonas spp. 1	m m o o	c c m o	m	c m m o o	c m o
L. aestuarii	c c m m o o	c c m o o o	o o	m	c o
A. oscillarioides		c o o		c o	c o
S. lardacea	c m	o	o o	c m o	c
H. virgata		c m o			
Navicula spp.	c m	c c m o o		c	
C. humicola	m	c			
Chlorococcoid organism	c o	c o			c

TABLE III. Continued

	A		*B*		*C*
	Pod MAM	Pow MAM	Cod MAM	Cow MAM	Pnd MAM
P. botryoides	m	c			c
S. Hofmanii				c	
Fremyella spp.		c			
D. Smithii		c			
S. muscorum				o	
S. ulna		c			c
U. flaccida	m o	m			
Anisonema spp.		c			

developed more quickly and grew more luxuriantly than colonies in the cistern water. Mineral and organic solutions provided about the same results.

The philosophy of the employed treatment and examination was to keep the soil reasonably close to field conditions. It was feared that culture conditions would affect both total flora and individual algal morphology. Yet, practical considerations of time and effort demand expeditious methods of obtaining identifications. It was desired to know whether the flora or morphology would be different when cistern water, mineral solutions, or organic solution were used. No discernible difference appeared other than the more rapid growth in the enriched solutions already mentioned. However, the characteristic morphological forms described in taxonomic literature for such genera as *Nostoc, Schizothrix,* and *Microcolcus* often do not develop until after a prolonged growth period and after some desiccation, and their recognition is difficult otherwise. It requires some experience to identify them correctly after as little as one month's development.

SUMMARY

The soil algae of the plow layer in two areas near Norman, Oklahoma, were studied through a spring season with the view of providing useful information in techniques of collecting, treatment,

and examination, to use in a planned survey of soil algae in central Oklahoma. Three collecting procedures—surface, auger, and solid core—were compared and found to be similar in results. The flora was similar in composition throughout the plow layer, although usually more luxuriant near the surface. Two unplowed grassland plots in different locations and a cultivated plot adjoining one of them contained an essentially identical flora. The flora did not change in composition from late March to late May. Enrichment of soil cultures with mineral solution or organic solution speeded development but did not otherwise affect the common flora. Illumination by either white or daylight fluorescent tubes (about 50-200 candlepower) yielded the same result in growth.

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THE MEASUREMENT AND VALUE OF PLANT HEIGHT IN THE STUDY OF HERBACEOUS VEGETATION[1]

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During the course of studies on the structure and changes in the California annual grass type, differences in plant height appeared in various treatments and years. Accurate, objective measurements of height were needed. A search in the literature failed to reveal clearcut information on procedures of sampling for height, on how to measure heights of plants of different growth forms, and in fact, the concept of plant height itself seemed confused. This paper explores the concept of height, mentions some of the difficulties in the accurate measurement of height, discusses the usefulness of height measurements, and describes a new method whereby the point-plot system may be employed to obtain an objective sample of height of plant materials. The term "plant materials" is significant and will be explained later.

[1] The data in this paper were collected as a part of Project 1501 in the California Agricultural Experiment Station.

Definition

Webster defines height as "the distance to which anything rises above that on which it stands; the measure upward from a surface, as the floor or the ground, of a man or an animal." Three points are clear in the definition. There is only one height of an individual. It is maximum; therefore, "height" and "maximum height" are synonymous. The second point is that "rises above" and "meas-

ure upward" denote perpendicular distance. Natural position is implied. The height of a man is the distance from the floor on which he stands to the top of his head—not to the tip of his finger when his arm is extended above his head. When these concepts are applied to an individual plant the definition becomes: The height of a plant is the perpendicular distance from the soil at its base to the highest point reached with all parts in their natural position.

The terms "average height" and "maximum average height" must be used carefully. Individuals of a plant species differ in height, so average height of a species denotes a mean of single measurements taken on several plants. In this sense the word "maximum" is excess wordage and average height is the proper term. On the other hand, when several average heights are being considered, the greatest of them is maximum average height. The least of them would be the minimum average height. Together they constitute the range of means; just as maximum and minimum heights must be reserved for the tallest and shortest individuals of an array from which a single mean is calculated.

The concept of height has not always been used in the precise manner of Webster's definition in the reports of research on vegetation. First, plant heights are difficult to determine. Second, viewpoints differ as to which plants should be measured to characterize the height of vegetation. Third, the principal value of height is to symbolize such qualities as vigor, stage of growth, site classification, and range readiness. Measurements other than "maximum" height may serve these purposes as well or better than those taken according to Webster's definition.

Difficulties in Measuring Height

Many factors impede the measurement of height in the precise manner specified by Webster's definition. The highest point may be difficult to find when plants are trailing or drooping, when the top is the tip of an awn, and when several parts are nearly the same height. If the highest part is not perpendicular from the base of the plant, an offset measurement is needed. In that case, configuration and slope of the ground surface hinder the taking of an accurate measurement. The base level must be defined arbitrarily for pedestaled plants. Wind and temporary wilting change the position of plants and they may be weighted down with a load of rainwater, dew or snow. Lastly, individual plants in such life-forms as rhizomatous grasses and rosettes are often inseparable from a patch of many plants. What appears to be a single bunchgrass may actually be several plants.

Perhaps these difficulties are indicated by the fact that seldom have procedures of measuring height been described in publication. For example, the statement, "Average height of leaf growth was measured to the nearest 0.5 cm.," does not tell whether the leaves were measured in natural position or straightened to their full length. Does the average, calculated to the nearest 0.5 cm., indicate that the actual measurements were taken to 0.5 cm.? How many measurements were taken to compute the average? In another case, the statement, "Height measurements were taken"; and the table heading, "Height of . . . ," do not tell whether leaves or stems were measured; yet separate grass plants, some with culms and some without, were shown in a photograph. Neither do these statements tell how many measurements were made and whether the data in the table are averages or single measurements. If heights are important enough to present in publication, the procedure for obtaining them should be described.

Concepts of Height

Most people have a general idea of the height of familiar things. That concept is close to Webster's definition when it is applied to individuals. When the items are in groups, as expressed by the words lawn, forest, and vegetation, the concept of group height varies widely.

Seventeen people including research workers, secretaries, students, and a janitor were shown Figure 1 and asked: What is the height of this example of vegetation? Their answers varied from 5 to 12 inches, and were based on various interpretations of the question. One used Webster's definition to express the height of vegetation as the height of its highest part, 12 inches. All the others reasoned that since vegetation is composed of individuals the height of vegetation should be an average. But here their viewpoints differed widely as to what should be included in the average.

The mean height of the dominant plants was considered by some, and their estimates averaged 10.3 inches. The average height of the 4 tallest plants in Figure 1 is 10.6 inches. This viewpoint may be the basis for the statement found in several papers to the effect that "Average heights of leaves and seedstalks were determined by measuring the 5 tallest in each plot." Others who examined Figure 1 included the dominants and subdominants in their estimates and one person mentioned the height of all plants.

The lowest figure given, 5 inches, was more with

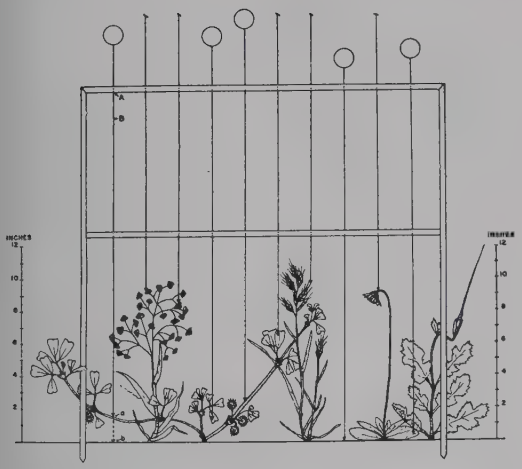

FIG. 1. This frame with 10 pins illustrates diagrammatically the point-plot method of sampling vegetation in the Californa annual type. Data from the example are given in Table I and an explanation is in the text. Plants illustrated from left to right at the soil surface are *Briza minor, Medicago hispida, Bromus mollis, Hypochoeris glabra,* and *Erodium botrys.* The scale along each side gives the reader an opportunity to compare his own estimate of height with those mentioned.

regard to the thickness or volume of plant material than to the actual height of individuals. In field application, it is the height of that point where one can see horizontally through the vegetation for a reasonable but unstated distance. Put another way, it is the average height of a large proportion of all the plant parts.

A related concept mentioned by some people in the discussion of Figure 1 was concerned with the length of stems and leaves. None confused this idea with height, but there is room for confusion of length and height in statements like: "The heights of grass leaves were measured after they were raised to their maximum length." Length measurements of plants seem more likely to be referred to as height than vice versa. Length of some plants is undoubtedly easier to determine accurately than height, and for purposes of measuring rate of growth and vigor length may be the best measure. However, if length is measured, it should not be called height even if it was measured as a perpendicular distance from the ground.

The varied interpretations resulted because the observers unconsciously gave different answers to three questions: What is the usefulness of height measurement? What constitutes the vegetation? How should height be measured? The different answers were indicative of the diverse training, interests, and approach among the group. To standardize the answer to any one of the questions is undesirable because that would tend to stereotype answers to the others. This is based on the premise that each objective has a best-method and each method is best suited to one or more objectives. There is little justification for saying that one method is better than another; except when stipulations of objectives and population are also given.

Each of us builds on what others do; part of our research job is to make that building as feasible as possible for the next person. Rather than standardize methodology, a better approach is to answer completely the three questions whenever experimental results are presented. These answers would be along the lines of: (1) clearcut statements of objectives, (2) definition of the population being considered, and (3) accurate descriptions of the methods employed. If this were done, few questions would arise as to the nature of the data.

Methods of Measuring Height

Height measurements have been taken in three different ways, although not without variation in the procedures with respect to type of equipment and accuracy of determination. Fortunately only one kind of measuring unit is employed—distance.

Frequently ocular estimates of height are made. They are difficult to define because the observer often tries to average in his "mind's-eye" the heights of several plants of a species or even of a plant community. Sometimes intentionally, he omits the exceptionally tall or short individuals from the estimate. The results may be sufficiently accurate for the purpose intended, especially if the observer is experienced and has trained himself with actual measurements. The procedures followed need to be accurately described so that another person may duplicate the study and make accurate comparison between his work and that already pubilshed. Ocular estimates are difficult to duplicate in the exact manner of another person.

A second procedure is to place a ruler alongside the plant to be measured and to read the height of the plant in its natural position. The factors that cause inaccuracies have been mentioned.

The third procedure is to straighten the plant to its fullest length and to measure that length with a ruler alongside. This measure eliminates the idea of natural position and should be described as length even though it may be height in some cases.

Usefulness of Height Measurements

Height of plants has been used by many investigators with numerous objectives in their

studies. Nearly all have used height as a basis for interpretation of characteristics such as growth, vigor, competition, etc. A few have given height data for its descriptive value and without reference to comparisons of treatments and conditions.

Growth: The rate of growth and the annual cycle of growth is well illustrated by McCarty, 1938; and McCarty and Price, 1942, who measured height at 5-day intervals and used the data to plot the annual growth cycle and to describe the relationship between growth and the chemical composition of plants. The differences in growth of plants in response to differences in weather have been shown by Sampson, 1918; Hanson, et al., 1931; Nelson, 1934; Lister and Schumacher, 1937; Tisdale, 1947; and Arnold, 1955. Growth of plants in pots of several kinds of soil was given on a basis of height by Joy, et al., 1954.

Vigor: Many studies where height has been used have attempted an estimation of vigor in one way or another. These usually are concerned with the relative response of plants to different experimental treatments. The treatments may be reseeded species under grazed and ungrazed conditions (Hull, 1944); pastures grazed by different systems of management (Hanson, et al., 1931 and Sarvis, 1923); burned and unburned conditions (Hervey, 1949); various frequencies and intensities of clipping forage plants (Sampson and Malmsten, 1926; Holscher, 1945; Whitman and Helgeson, 1946; and Weaver and Darland, 1947).

Competition: Height of plants was used as one of several criteria to determine the degree of competition between 17 seeded species and *Artemisia tridentata* (Robertson, 1947).

Adaptability: Comparisons of height attained by different species on the same habitat and within one species on different sites has been used widely in the study of adaptability of forage species to new areas (Hull, 1954; and Potter, 1955).

Resistance to grazing: Branson (1953) presented data which showed that the height to which growing points in grasses was elevated above the ground was related to resistance to grazing. Much of the work listed under vigor also has application in studying the differential response of species to grazing.

Range readiness: Height of important forage plants is the best indicator of the time when ranges are ready for grazing (Costello and Price, 1939; and Craddock and Forsling, 1938). Studies of the effects of various frequencies and intensities of clipping forage plants have practical application in the determination of the date of range readiness.

Forage utilization: This subject has received considerable attention and several methods are available for measuring degree of forage use by livestock. Comparisons of height between grazed and ungrazed plants is an important feature in most of these methods (Heady, 1949).

Range condition and trend: For several years height of plants has been used in the evaluation of trend of range condition. Short-run changes due to yearly differences in weather are indicated by heights of leaves and stems. Parker (1953) has given a procedure whereby height changes due to grazing treatment may be separated from those due to weather. These are indicative of short-time trends in range condition and even though a large amount of personal judgment is required the concept is a useful one.

Site classification: In forest management a timber site may be defined by the timber growing capacity. Growth is indicated by height for age of the dominant trees and this is the primary basis for timber site classes (Dunning, 1942). Tree height is measured by means of an Abney level and tape.

Yield: Often there is a close correlation of the height of plants and the dry weight or bulk. Klages (1942) found the correlation coefficient to be greater than 0.9 on numerous occasions. This allows successive approximations of weight of the same plant.

The concept of height is embodied in several terms in plant ecology although actual data for height of plants or plant communities is seldom given. A few of them are dominants and subdominants, layer societies, life-forms, and seasonal aspects. Actual data on height would add to the descriptive value of these and other terms.

The Point-plot Method of Determining Height

The point system was found to be an accurate and objective procedure for determining percentage botanical composition in the California annual-type. Briefly, the method of determining height was simply to ascertain the height of the first hit above the soil surface. This distance was measured along the pin. When the point first touched a plant (point a in Figure 1) as it was gently pushed through the vegetation, the location on the pin where it was protruding from the upper cross piece of the frame (point A) was held by the thumbnail. After the point had touched soil (point b) the distance A-B, between thumbnail and frame, was measured with a steel tape. This distance was equal to the distance between the hit and the soil surface, a-b.

The data constitute a sample of the heights of every bit of plant material the size of the pin

point. The pins are maintained at needle sharpness so the heights for all practical purposes are of infinitely small spots on the plants. The spots vary in location from 0.1 inch above the ground, the minimum recorded, to the very top of some plants. For want of a better term, the data are referred to as "heights of plant material."

The data are indicative of the height of mass within an individual plant or a species. Likewise, the concept may be applied to the whole vegetation by summarizing without regard to species. The method furnishes data for determining the relative vertical position of species in a stand. In short, it gives a vertical dimension to the concept of foliage cover.

There are several advantages to the method. It is objective in that the observer exercises little choice in what is measured and how. The sample may be random or systematic according to the desires of the investigator. Many readings can be made cheaply and easily. The sampling for height can be done in conjunction with the sampling for other types of information obtained from the points. For example, the same set of pins may be used to determine foliage cover, cover repetition, percentage botanical composition, mulch cover on the soil, and height. Sampling can be done by one man although two will relieve the tediousness of the job. In terms of output, two men, each working separately, will gather more data than two men working together.

For purposes of illustration; the set of 10 pins in Figure 1 is summarized in Table I. The foliage cover is 90 percent. *Medicago hispida* contributed most to the percentage botanical composition and at the same time was lower in height of materials than the other species. The two grasses were tallest but low in composition. The average height of plant material in the whole vegetation was 5.2 inches. The fifth species, *Erodium botrys* would undoubtedly have been included if the sample had been larger.

Data previously published indicate that height of plant materials and forage production in the California annual type were closely correlated with amount and position of mulch (Heady, 1956). Heights were taken with the point-plot method.

Many individuals, tall and short, of many species compose vegetation in the California annual type. These data (Table I) illustrate a procedure whereby a relative measure of their height may be obtained. If height in this sense is usful for individual species it can also be an important characteristic of the whole vegetation. The remainder of this paper is given to three examples of the use of this method in field scale studies.

TABLE I. Percentage botanical composition and average height of plant materials in inches for the example shown in Figure 1

Species	Number of hits	Composition in percent	Avg. Height in inches
Briza minor	2	22.2	8.9
Bromus mollis	1	11.1	7.7
Hypochoeris glabra	2	22.2	4.9
Medicago hispida	4	44.5	3.0
For all vegetation	9	100.0	5.2

The work was done in the annual-type vegetation on the Hopland Field Station in Mendocino County, California. The natural vegetation is seldom more than knee high and many plants of many species are present. There may be as many as a dozen mature plants per square inch with several species represented. Most of the leaves are small but there are infinite numbers of them. The method of measuring height described has not been attempted on other vegetational types but it should be effective wherever the point system is practical.

Comparisons Between Areas

Several experimental pastures about 40 acres in size have been established on the Hopland Field Station to test grazing practices. The initial inventory which in part consisted of sampling for percentage botanical composition and height of plants showed all the pastures to be similar. Data from two pastures are given in Table II.

TABLE II. Average height of plant materials in inches and percentage botanical composition on two similar pastures as determined by the point system

	Pasture 1		Pasture 2	
	Average ht., inches	Composition in percent	Average ht., inches	Composition in percent
Bromus rigidus	5.3	6.5	6.0	6.4
Aira caryophyllea	4.8	26.7	4.6	20.9
Daucus pusillus	4.8	7.9	4.3	3.0
Bromus mollis	4.7	22.5	5.0	21.8
Erodium botrys	3.3	15.0	3.1	16.2
Trifolium microdon	3.0	2.4	4.0	5.1
Trifolium microcephalum	2.6	5.6	2.5	2.5
Festuca dertonensis	2.4	2.4	3.4	8.5
All others	3.9	11.0	4.4	15.6
Average heights	4.3	....	4.3	

Variation occurred between pastures but it was not significant for the major species either with respect to composition or height. The average height of vegetation was essentially the same in all the pastures. In addition, the percent of ground surface covered by plants was 44.2 in Pasture 1 and 48.7 in Pasture 2. Not only do these data characterize the degree of similarity of the pastures

but they will serve as the reference points to evaluate vegetational changes as the grazing trial develops.

In addition to the use of height to assess differences in areas at one time and over time mentioned previously, the height relationship among species within a study area is obtained. Within the two pastures (Table II), *Bromus rigidus* is the tallest species, except for *Avena barbata* which is included in the group "all others." These two species give the vegetation a characteristic appearance because their height makes them the most conspicuous. In terms of botanical composition, *Aira caryophyllea, Bromus mollis,* and *Erodium botrys* were clearly the most important. The question of which group is dominant is an interpretative point of little importance when the species are described by both measurements.

The fact that some species are tall, some short and others intermediate is perfectly obvious. The use of layer societies to describe the situation is a common practice. However, a glance at the average heights by species (Table II) indicates that definite layers do not exist in this example of the California annual type. Rather, there is a continuous range of heights within one area at a given time. The range of plant heights in the California annual type changes each year (Table III) and during the growing season (Table IV). This vegetation, then, lacks clear-cut vertical layers.

TABLE III. Average height of plant materials in inches for annual plants at the same location and dates in three years

	May 1 1953	April 29 1954	April 29 1955
Bromus rigidus	4.2	9.3	2.2
Bromus mollis	5.5	7.2	2.5
Erodium botrys	2.8	5.1	1.5
Erodium cicutarium	3.4	3.9	1.7
Briza minor	2.2	7.5	1.3
Trifolium microcephalum	2.1	5.9	0.4
Trifolium ciliolatum	1.1	3.6	1.8
All others	3.3	5.3	2.1
Average	4.2	6.5	2.0

Comparisons Between Years

The heights of plants by species was measured near the end of the growing season in the same area for three years (Table III). The differences in height due to differences in weather conditions are brought out. All the plants grew very well in 1954 when there was an even distribution of rainfall in late spring. *Bromus mollis* and *Bromus rigidus* contributed approximately 60 percent of the composition. In 1955 there was a prolonged early spring drought and total plant growth was less than in 1954. *Erodium botrys,* a low growing species, was more abundant and the grasses less abundant than in the previous year and, hence, the low average height of vegetation in 1955. The data for height by species and average height for the whole vegetation give an additional measure of the vegetation that is helpful in describing yearly changes in vegetation.

Comparisons Between Types, Seasons, and Grazing Treatments

Table IV is presented to illustrate the usefulness of height in the description of different vegetational types, of seasonal changes, and of utilization of forage by livestock. The data were obtained by sampling a pasture of approximately 200 acres in size which was grazed by sheep from March 1 to May 10, 1955. A total of 1890 points was taken on March 8, on June 7-8 in areas protected from grazing, and on June 7-8 in grazed areas. The grassland type had no trees and the open woodland had a scattered stand of oaks with an understory similar to the grassland type.

TABLE IV. Average height of plant materials in inches of annual plants in a grassland and open woodland for March 8, ungrazed, and June 7-8, grazed and ungrazed, 1955

	GRASSLAND			OPEN WOODLAND		
	March 8, 1955	June 7-8, 1955		March 8, 1955	June 7-8, 1955	
		Ungrazed	Grazed		Ungrazed	Grazed
Avena barbata	1.5	12.1	6.5	1.3	6.1	5.5
Bromus rigidus	1.2	9.4	4.6	1.3	6.9	3.6
Bromus mollis	1.2	5.6	3.1	1.2	3.8	2.9
Aira caryophyllea	0.8	5.0	2.8	0.8	4.6	2.9
Daucus pusillus	1.1	4.7	3.5	1.1	4.2	2.8
Erodium botrys	0.7	4.5	2.4	0.7	4.6	2.3
Trifolium microcephalum	1.0	3.0	1.7	...	2.2	2.2
Trifolium ciliolatum	1.0	2.0	3.2	1.4	1.9	2.2
All others	1.1	3.5	2.5	0.9	3.3	2.8
Average	1.0	4.2	2.8	1.0	3.9	2.8

The average height of plant materials was essentially the same in both vegetational types throughout the growing season and only minor differences occurred in the botanical composition. The grasses were slightly more in percentage composition in the grassland. Exceptions were *Stipa lepida* and *Cynosurus echinatus,* which were restricted to partially shaded areas. Several broad-leaved plants were more common in the shade than in the open. There were very few species that did not occur in both types.

The heights of individual species varied considerably between types. *Avena barbata,* for example,

was about twice as tall in the open and *Bromus mollis* about a third taller than in the shade. *Erodium botrys* was the same height in the two types. Others such as *Navarretia, Filago, Hordeum* and *Sanicula* were taller where partially shaded.

Foliar density was approximately 55 percent in both types. The herbaceous cover in the two types was very similar. There were slight differences in percentage botanical composition and some species were different in average height between the two types.

Seed germination of most species occurs immediately following the first fall rains. Growth is slow during the winter but the species grow in height at different rates. On March 15 the 4 grasses in Table IV had attained 12 to 24 percent of their height in the grassland and 17 to 31 percent where there was a partial canopy from trees. Other species showed a similar trend of attaining a larger proportion of their growth at a given time in partial shade than in the open. The actual height of plants in the two types was low and nearly the same in March. Greater differences among the species developed as the fruiting stalks elongated in late spring.

Grazing by animals reduces the height of vegetation. In 1955 the heights of plants both inside and outside small cages were measured. The reduction in height due to the activities of animals was 33.4 percent in the grassland and 28.2 percent in the open woodland. Utilization by weight for the two types was 42.3 and 37.4 respectively. In terms of the whole pasture there was a difference of five percent in the measurement of utilization by the height method and by the weight method. Tests in previous years and at other locations showed that both procedures indicate the trends in utilization but that large differences in the actual values are likely to occur.

Summary

1. The meaning of such terms as "height," "average height" and "maximum average height" is given in relation to a proposed definition of plant height: The height of a plant is the perpendicular distance from the soil at its base to the highest point reached with all parts in their natural position.

2. Different concepts of plant height and difficulties in measurement are suggested as the reasons why procedures for measuring height are seldom given in publications.

3. Stipulation of a best method to measure height can only be done after the experimental objectives and definition of the population have been provided. Clear statements of objectives, experimental material and methodology facilitate the gathering of comparable data as well as reduce questions which arise as to the nature of the data.

4. Methods of measuring height and the usefulness of height measurements are reviewed.

5. A method of measuring height of plant materials with the point-plot method is described. The data characterize the height of mass for species individually and for vegetation and provide a measure of the vertical position of a species in a stand. The point-plot method is used to determine foliage cover and the additional measurement of height with the same pins gives a vertical dimension to that cover.

6. The advantages of the point-plot method in determining height include objectiveness, ease in operation, and the addition of another measurement to those normally collected with the point system.

7. Examples of field data are given to illustrate how the method may be used to compare species and vegetation between areas, years, seasons, vegetational types, and grazing treatments.

8. Even though field application has not been attempted outside the California annual type, the method should be useful wherever the point system is applicable.

9. There is a continuous range of heights of plant materials for the many species in the California annual type rather than clear-cut layers of vegetation.

10. Height of plant materials has intrinsic value in the description of vegetation when sampled by the point-plot method.

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INFLUENCE OF TEMPERATURE UPON SOIL MOISTURE CONSTANTS AND ITS POSSIBLE ECOLOGIC SIGNIFICANCE

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The fact has been well established that on the basal plains surrounding the Rocky Mountains, soil drouth penetrates deeply and persists for several months each summer. With increasing elevation this aspect of drouth becomes progressively less intense, until at elevations corresponding with forests of *Picea engelmanni* and *Abies lasiocarpa*, if not before, it is far less critical as a factor determining seedling survival (Daubenmire 1943). The soil moisture gradient has been explained as the net effect of (1) an increase of precipitation with altitude, (2) decreasing intensity of factors promoting plant use of soil moisture (Sampson 1918; Whitfield, 1932), and (3) a shortening of summer.

The first of the above factors has limited significance on the westerly slope of the northern Rockies for the fact that summers are essentially rainless at all altitudes, the vertical increase in annual precipitation being primarily a result of high snowfall which comes at a time when the environmental water-balance is not critical. It is significant to note that this places no handicap on the vegetation, for the soils of subalpine regions support communities fully as mesophytic as in any other part of the Rockies even where rainfall is relatively heavy in summer. This circumstance tends to shift the explanation of continued high moisture levels to factors 2 and 3. During one summer when the moisture content of high-altitude soils was being sampled at regular intervals, it occurred to the writer that still another factor might add its weight to those mentioned, and a test of this hypothesis resulted in the studies reported below.

It was noticed that in late spring soils not much above freezing were patently moist when removed from a pit with a trowel, but after the soils were transported down to the warm regions of the basal plain and weighed in a laboratory the metal

cans often had considerable free water. Since it has been shown that temperature influences soil moisture movement through its effect upon viscosity (Gustafsson 1940, Pillsbury 1950), it occurred to the writer that in spring the soils at high altitude may hold more water than the mechanical properties alone would indicate, then as the soils slowly warm during the summer this surplus of water might make a material contribution toward delaying the attainment of the wilting coefficient.

Temperature Influence upon Water-holding Capacity

The fact that the water-holding capacity of soils decreases as temperature increases was shown by Bouyoucos in 1915. Gustafsson (1940) pointed out that all permeability studies should be referred to a standard temperature, and Richards and Weaver (1944) showed that a lowering of temperatures increased the water held by soils in pressure membrane tests conducted at 0.5 and 15 atmospheres. No one appears to have considered this phenomenon important in plant ecology. In order to obtain more information on water movement through soil as influenced by temperature, a lysimeter was made consisting of a column of builder's sand approximately 45 cm tall by 15 cm in diameter, contained in a metal cylinder with a funnel soldered to the lower end. Wire gauze covered with absorbent cotten was fittted into the funnel at the constriction so that sand particles would not be carried down with the leachate. This lysimeter was closed off temporarily at the bottom with pinched rubber tubing, water added to bring the water-table level with the surface, a hot wax film poured on to the seal against evaporating, then set in a refrigerator at a temperature just above freezing. After temperature equilibrium was attained the pinch cock was removed and water allowed to percolate until dripping practically ceased, the percolate being measured at intervals. Next the temperature was allowed to rise to approximately 25°C, and the renewed percolation measured (Fig. 1).

Two moisture equilibria in the soil are clearly demonstrated, these being attributable to different temperature levels. This experiment was repeated several times in an attempt to obtain closer temperature control, but this proved impossible with an experiment extending over a 5-month period depending upon a household refrigerator located in a building where frequent remodelling necessitated temporary interruptions of electricity. However, all results were consistent with Figure 1 in showing a definite increase in yield whenever temperature was raised.

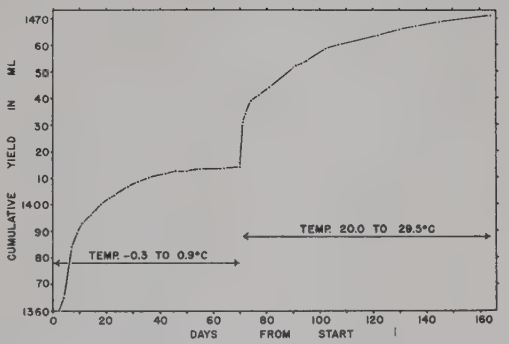

Fig. 1. Cumulative water yield from a lysimeter containing sand saturated until time zero.

The oven-dry weight of the sand used was 12.77 kilograms. This volume of material yielded approximately 55 ml of gravitational water within 94 days as the temperature rose approximately 25°C after the first equilibrium was reached. It is interesting to calculate the yield of a square meter of sandy soil one half meter deep in terms of equivalent rainfall, as an aid of visualizing the significance of this phenomenon under natural conditions.

Assuming the volume weight of the sand to be approximately 1.7, a square meter of sand one half meter deep weighs 850 kg, and according to the results described above (12.7 kg yielding 55 ml) this would yield 3.6 kg water as the temperature rose from 1-25°C. The precipitation equivalent is 3.6 mm.

In evaluating this quantity one must remember that *all* such liberated water is available to plants because, unlike snow, rain or dew, none is intercepted by foliage and A_0 material, and thus lost. Furthermore, the material used, builder's sand, has an extremely low water holding capacity, and the yield of an equivalent volume of loam would be considerably more than this amount. When both these factors are taken into account, it appears that the yield of water made available by the gradual increase of temperature throughout summer in cold forest regions might make a material contribution to the supply of readily available water. It would be especially significant where the summers are rainless, as they are in this part of the northern Rockies. Since shade provided by the trees at high altitude materially slows the rate of heat absorption by the soil, one might expect conditions in burned-over areas to differ, at least in the surface horizons. Probably here, and certainly in the grasslands of the basal plain, the heat-released water is freed long before it is needed by plants, with a result that it may be

lost by percolation to levels below the reach of roots or wasted as "luxury consumption."

Influence of Temperature upon the Moisture Equivalent

Veihmeyer et al. (1928) showed that temperature has some influence on moisture equivalent determinations, and recommended that determinations should be made with temperatures near 20°C. Owing to the stated objective of their study, they were not concerned with the possible significance of temperature influence as it might affect the interpretation of data from habitats with very cold soil. Others have subsequently tended to ignore temperature considerations altogether when discussing the moisture equivalent.

Four soils exhibiting a wide range of moisture holding capacities were assembled and screened to uniformity. Each test was in quadruplicate since the standard centrifuge employed has a capacity of 16 samples. A vibration tachometer was used continuously as a guide to manipulate the rheostat so as to maintain a force of 1000 gravities as closely as possible. The soil boxes were filled to a constant depth by a template so adjusted as to stroke off the surface leaving a layer of dry soil of about 15 mm depth, experience having shown that such a layer compacts to about 10 mm upon wetting and centrifuging. In both of the contrasted series of determinations the soils were moistened and allowed to hydrate in a humid atmosphere at room conditions (appx. 25°C) for 24 hours. The warm series was then centrifuged at the same temperature. To make the cold series of determinations, the soils hydrated first in the warm room were allowed to come into equilibrium with the temperature in a room kept at 1.5°C. The centrifuge had already been chilled to this level.

The results (Table I) show clearly that the colder the soil the higher the moisture equivalent, the difference being slight in sand but amounting to 1.39% in the soil with highest water retentiveness. If the field capacity is approximately equal to the moisture equivalent in a loam, then shortly after the snow has melted in spring, the field capacity may be approximately 1% higher than at the end of a hot dry summer, at least in the surface horizons.

Assuming a volume weight of 1.6 for a loam, a square meter of soil one half meter deep would weigh aproximately 800 kg, and the experimental results indicate that the warming of such a mass of soil from 1.5°C to 28° would release 8 kg equalling 8 mm of precipitation. This thermal yield is twice that calculated for the lysimeter experiment,

Table I. Influence of temperature upon moisture equivalent percentages

Soil Material	Moisture Equivalents and Medians				Increase due to chilling
	28°C		1.5°C		
River sand	2.61 2.66 2.70 2.71	2.68	2.81 2.85 2.90 3.98	2.88	0.20
Silt loam, light yellow subsoil	20.31 20.45 20.81 20.94	20.63	20.91 21.19	21.05	0.42
Clay, B_2 of planosol, high in Na	34.03 34.17 34.32 34.40	34.24	34.73 35.07 35.07 35.24	35.07	0.83
Silt loam, with high humus content	35.87 35.90 36.28 36.72	36.09	37.07 37.17 37.79 37.98	37.48	1.39

owing to a greater temperature differential and a higher water retaining capacity.

The differences of 0.2 to 1.39% in moisture equivalent obtained by centrifuging four soils at 28 and at 1.5°C, are closely similar to the results of Veihmeyer et al. (1928, Table 18) who found that centrifuging four soils at a range of 21-26° and again at range of 1-10° increased the values 0.7 to 0.9%. From the writer's data it seems that high humus content has a marked effect of increasing water retention of soils under low temperatures.

Temperature Influence upon the Wilting Coefficient

Since soil moisture constant determinations do not assume significance in plant ecology until they are related to field capacity and wilting coefficient, the foregoing studies suggest that an inquiry be made into the possibility that temperature may need equal consideration in our conception of the wilting coefficient.

A number of investigators, starting with Sachs in 1870, have found that plants may be wilted simply by chilling the soil in which they are rooted. Clements and Martin (1934) found that the rate of water absorption by plants increases directly with temperature up to about 30°C. This phenomenon has two distinct aspects, one dealing with protoplasmic response to low temperature as this affects absorption and transmission through cells, the other concerning the mechanics of availability of water in soils. Kramer (1934) has shown that the ability of a moist soil to deliver water to an absorptive surface increases as the temperature rises. Hendrickson and Veihmeyer

(1945) found that with both tops and roots at 55°C, the wilting coefficient for *Helianthus* was the same as with both tops and roots at 75°C. However, with tops maintained at room temperature and root temperatures varying from 41 to 55°C, there was a decrease in wilting coefficient of 0.5% (fine sandy loam) at the higher temperature. The difference was so small that it was considered inconsequential.

Helianthus annuus and *Triticum sativum* were grown together in loam screened to uniformity in two groups of glass tumblers so arranged that the environments differed only in soil temperature. The technique described by Daubenmire (1947, p. 128) was followed, except that the tumblers were set in holes cut in water-proofed cardboard that fitted snuggly around the rims of the tumblers. One series of tumblers was submerged almost to the cardboard in cool water, the other was arranged to form the top of a box in which the air was maintained at a uniformly high temperature by means of a thermostat and heating element. A number of cultures were started on a greenhouse bench, then two uniform series were selected and transferred to the contrasted environments, after which they were given several days to become acclimated, under somewhat optimal conditions of soil moisture. Then watering was discontinued and the soil surfaces sealed over with paraffined cardboard and modelling clay. Permanence of wilting was determined for each tumbler independently using wet cloths hung vertically in the chambers but without changing the positions of the plants. The results of this experiment (Table II) show that a differential in soil temperature of 12°C (17.5-29.5) with air temperatures at approximately 20-25°C causes a difference in the wilting coefficient amounting to 1.2%. The experiment was repeated several times using different plants, and similar results were obtained consistently. The value obtained was slightly more than twice the value obtained by Hendrickson and Veihmeyer (1945), under roughly comparable conditions.

If it appears that the effect of soil temperature upon the wilting coefficient is small, it should be remembered that 1.1% moisture in a square meter of a loam one half meter deep represents approximately 8.3 kg water or 8.3 mm of precipitation. A small percentage figure is thus surprisingly deceptive in this respect. The conclusion, therefore, seems warranted that for maximum accuracy in interpreting the moisture contents of soils obtained in the field, the wilting coefficients should be determined by duplicating soil temperature conditions as determined in the field at the time the soils were collected for moisture analysis.

TABLE II. Influence of temperature upon wilting coefficients. Eight simultaneous replications

WILTING COEFFICIENTS AND MEDIANS			
15.6-19.5°C		29.0-30.0°C	
10.13		9.08	
10.07		8.79	
9.94		8.67	
9.63	9.60	8.64	8.51
9.57		8.39	
9.57		8.38	
9.53		8.29	
9.38		8.18	

DISCUSSION

Although the small influence of temperature upon soil moisture constants has long been recognized, its possible significance in plant ecology has never been pointed out. Perhaps this is a result of underestimating the actual quantity of water represented by only one or a few per cent.

In the *Picea* forest where the water content determinations were made that prompted the present study, the average moisture equivalent of the upper five decimeter-horizons of the mineral profile is 38% and the wilting coefficient 16.5%. During the rainless summer period the soil temperature of this layer was found to rise from about 2 to 10°C. Judging from the data in Table II, one could expect nearly a 1% drop in the wilting coefficient during the summer, which alone would make available water equal to about 8 mm of precipitation. To this must be added the extra increment of water retained due to low temperature in the spring, an additional 0.5% equalling approximately 4 mm of precipitation. If *Picea* forests transpire the equivalent of about 215 mm of precipitation a year (Raber, 1937), and heat absorption alone provides 12 mm during the critical growing season and this only in the upper 5 dm of the profile, the heat-released water may make a significant though small contribution toward maintaining growth water under these special conditions. This effect of postponing the attainment of the wilting coefficient would at least be equivalent to the influence of dew in retarding the rate of water utilization, which has been considered ecologically significant in other regions. Actually the 12 mm is about equal to the average amount of monthly rainfall in summer in these *Picea-Abies* forests. The mean July rainfall of 12 stations varies from 16 to 41 mm (0.6 to 1.6 inches), with the August rainfall varying from 13 to 24 mm (0.5 to 1.0 inches) (Daubenmire, 1956).

The errors involved in evaluating growth water storage capacity (field capacity minus wilting coefficient) using laboratory determinations of both constants would be of a low order of magnitude simply because both of the values are elevated above field conditions. But in evaluating water-holding capacity on a seasonal basis it is the field capacity in spring, under cool conditions, and the wilting coefficient toward the end of the warm season that must be compared.

The results also may have a bearing on interpretations of the diurnal pulsation in flow of small streams. Explanations of the phenomenon are usually based entirely on diurnal variations in the use of water by plants, which tends to interrupt flow toward stream channels. Meyer (1928, p. 392) states that "the daily rate of discharge of streams . . . may be prominently affected by temperature changes," and Clyde (1931, p. 21) found that "there was a marked fluctation in the stream discharge, due to temperature changes, in spite of the fact that the rate of snow drainage was constant."

Summary

It has long been known that at high altitudes the summers are shortened, the rate of water use by plants is reduced, and in many areas the rainfall increases. Experiments show that still another phenomenon favors water conservation: the seasonal march of temperature results in raising the field capacity in the spring and lowering the wilting coefficient in late summer, thus creating greater storage capacity than might be suspected if soil temperature were ignored. The increased storage in the rooting horizon is equal to about 12 mm of rainfall, and although this quantity is very small it approximates the normal rainfall of each of the two warmest months. Furthermore, in contrast with dew or precipitation, almost none of the temperature-released water is subject to interception, direct evaporation from the soil, or loss by percolation. Thus there are four complementary factors having cumulative effect that may be used to explain the ability of high-altitude forests of the northern Rockies to maintain growth water supplies during an essentially rainless summer of three months' duration. Possibly this phenomenon may also have a bearing on explanations of the rhythmic diurnal variations in streamflow that have been based entirely on transpiration.

Acknowledgments

This study has been supported by funds provided for biological and medical research by the State of Washington Initiative No. 171. I am grateful to F. J. Veihmeyer for offering helpful criticisms during the preparation of this manuscript.

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LANGUAGE ANALYSIS AND THE CONCEPT *ENVIRONMENT*

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"If you want to find out anything from the theoretical physicists about the methods they use, I advise you to stick closely to one principle: don't listen to their words, fix your attention on their deeds. To him who is a discoverer in this field the products of his imagination appear so necessary and natural that he would like to have them regarded by others, not as creations of thought but as given realities.

"These words sound like an invitation to you to walk out of this lecture. You will say to yourselves, the fellow's a working physicist himself and ought therefore to leave all questions of the structure of theoretical science to the epistemologists." (Einstein, 1934)

"Science is the attempt to make the chaotic diversity of our sense-experience correspond to a logically uniform system of thought. In this system single experiences must be correlated with the theoretic structure in such a way that the resulting coordination is unique and convincing.

"The sense-experiences are the given subject-matter. But the theory that shall interpret them is man-made. It is the result of an extremely laborious process of adaptation: hypothetical, never completely final, always subject to question and doubt.

"The scientific way of forming concepts differs from that which we use in our daily life, not basically, but merely in the more precise definition of concepts and conclusions; more painstaking and systematic choice of experimental material; and greater logical economy. By this last we mean the effort to reduce all concepts and correlations to as few as possible logically independent basic concepts and axioms." (Einstein, 1940)

If we substitute the words "ecologists" and "Ecology" for the words "physicists" and "science" in the above quotations from Einstein, we will have succinctly stated the problem we ecologists face in ridding ourselves of our confusions of ideas with realities and in translating our observations and experiments into communicable knowledge as a "logically uniform system of thought."

The development of Ecology has been characterized by many controversies that appear to us to be largely in the realm of words rather than deeds. This is not surprising, however, because the highly complex nature of the relations between the environment and organisms often leads to both frustration in interpretation and to vagueness in generalization. The aggregate nature of vegetation and the ensuing abstract conceptual complexities as they are necessarily handled in language, have contributed to a compounding of this confusion. Such perennially current questions as "Do communities really exist?", "Should the fundamental unit of study be the individual, the population, the community, or the ecosystem?", "Is the classification of communities desirable?", and "Is the ecosystem so complex as to defy significant analysis?" appear by their context to be resolvable largely upon the basis of additional empirical phenomena. But, in reality, they can be enormously clarified through a proper knowledge of our medium of understanding and communication without recourse to new facts. We have become convinced that where controversy reigns for long periods in science, in spite of the discoveries and new techniques developed by generations of scientists, the difficulty is probably not so much inherent in the material as in the language in which it is being discussed.

Language analysis provides an approach to the resolution of some of these difficulties. Several scientific fields have been illuminated by the use of these methods, the most prominent among them being physics and psychology. It seems to us that there might be some values here for the ecologist.

We have investigated, in particular, the Theory of Signs (Morris, 1938) and applied these methods to the language in which our various concepts of the environment have been expressed. As a result we have been led to a reappraisal of this key concept in the structure of ecological knowledge. Although we cannot here deal with the Theory of Signs in great detail, we would like to present a brief résumé before embarking upon our analysis of the concept *environment*.[1] We solicit patience with what may seem to be a tedious presentation of subtle details which we hope will give a background in the terminology and the concepts that we employ in our explanations. We hope that the reader will not leave us as Einstein thought his listeners might, convinced that this is not Ecology.

We wish to express our appreciation to David Rynin for many helpful suggestions in the formulation of our concepts, but we do not imply that he is in any way responsible for what may prove to be our misuse of them. Albert Ulrich read the

[1] Following semantic convention, the same word may appear in quotation marks, in italics, and in ordinary type. This indicates as the subject respectively the "word," the *concept*, or the phenomenon of nature.

manuscript and offered valuable suggestions. To Annetta Carter, Helen Sharsmith, and Francia Chisaki we are indebted for suggestions as to details of presentation and illustration.

Theory of Signs

According to Morris (1937) the Theory of Signs has assimilated the pertinent aspects of logical positivism, empiricism, and pragmatism, resulting in the resolution of language analysis into three aspects. These are the syntactic, the semantic, and the pragmatic. Syntactics establishes the relation of the sign to the sign, semantics, the relation of the sign to the object, and pragmatics, the relation of the sign to the user. These aspects are closely interrelated and yet represent coordinates useful for description. Thus they are generally referred to as "dimensions" of language (Fig. 1). In referring to signs we here are concerned only with words as employed as signs. For a lucid discussion of the differentiation of signs and symbols, the reader is referred to either Langer (1948) or Hospers (1954).

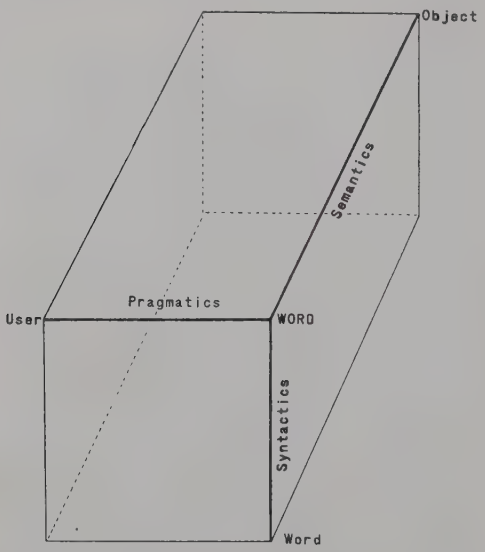

Fig. 1. Three dimensions of language as viewed in the Theory of Signs.

The syntactic dimension

The syntactic dimension has received more thought than either of the other two points of view. Scholars from the earliest times have been concerned with inference, and this by necessity involves the relations between combinations of signs within a language. The axiomatic or deductive system in Euclidian geometry is based upon a set of primitive propositions or premises from which a set of conclusions is derived. Systems of this sort made the development of syntactics inevitable. However, it was Leibniz, the mathematician, who saw that "linguistic, logical, and mathematical considerations led jointly to the conception of a general calculus giving a universal, formal method of drawing consequences from signs" (Morris, 1938). This unification and generalization of mathematical form and logical method has received, since Leibniz's time, extensive development in symbolic logic through the endeavors of such men as Boole, Frege, Peano, Pierce, Russell, Whitehead, and others. The theory of syntactical relationships has received its most elaborate development in the logical syntax of Carnap (1936-1937, 1937).

Logical syntax concentrates on the structure of langauge. In other words, a language becomes any set of signs (words) related or ordered in accordance with two classes of rules: 1) Formation rules which determine allowable independent combinations of members of a set of words or phrases (such combinations being called propositions, statements, or sentences). These rules are known to us familiarly as the laws of grammar. 2) Transformation rules which determine the sentences which can be obtained from other such sentences, i.e., rules governing implication or inference, and the other basic operations of propositional logic.

In most discussions of the Theory of Signs, syntactics emphasizes logical syntax, i.e. linguistic structure. In logical syntax classes and relations play an important role. This is because most of the words that we employ are class words, that is, they stand for classes of things or actions. The class itself is predicated upon some common property of the terms or some common relation of the terms to some other phenomenon. Statements employing class words express relations between such classes. Because, we employ such words in statements as signs related to signs, they are handled as formalities in logical syntax. The understanding of the theory of classes and the theory of relations is fundamental to all intellectual work, and is especially so in science, where we are striving for a precise language adequate to express these relations.

Classes are a part of an intellectual organization system generated by the observer to explain certain relations between what is being classified. There are many ways whereby things may be classified. However, in all, the basis of classification is some common denominator which becomes the defining property of the class. Any property or any com-

bination of properties may be defining. Where possible, properties which are intrinsic, i.e., properties that are inherent and do not depend upon the existence of other things, are made defining. For example, the defining properties of a chemical compound are the elements of which it is composed. But in many other cases it is not the intrinsic properties which are made defining, but rather it is certain properties which are extrinsic, i.e., properties which the thing has only in relation to other things. Thus what distinguishes the class of husbands from all other men is not any intrinsic properties of men, but rather their relation to wives. It must also be realized that in the theory of classes, it is possible to distinguish different levels of classes. A class of individuals constitutes a class of the first order or level, classes of the first level when aggregated constitute a class of the second level, and we may continue to classify to such levels as may be required. It is of the utmost importance to keep these levels distinct in our thinking because each level is based on a different combination of properties and is constituted of a different set of primary constituents. Each level comprises a different logical type.

A relation may be distinguished from a class by the fact that it always involves a predecessor and a successor. The **predecessor** is that which is related to something and the **successor** is that to which something is related. The class of all predecessors with respect to the relation in question is known as the **domain** of the relation, and the class of all successors is known as the **counter-domain** of the relation. The **field** of the relation is the logical sum of its domain and counter-domain. In the theory of relations, just as in the theory of classes, we may distinguish relations of different levels or orders. The first level may be empirical, whereas the second level may hold between classes or relations of the first level, and so on. The situation may become complicated by mixed relations, i.e., the predecesor may be a class of the first level and the successor may be a class of the second level. In these cases the concept *field* has little utility because it is not logically homogeneous, and if we employ it we become engulfed in a confusion of logical types.

Relations have properties by which they may be classified, i.e., symmetry, reflexivity, transitivity, and connexity. To our problems the relations of symmetry are especially significant. In a relation xRy where xRy implies yRx the relation is said to be symmetrical. Where xRy does not imply yRx the relation is said to be asymmetrical. The former type is significant to problems of identity and the later to the establishment of order in relations.

Among asymmetrical relations of great utility are those spoken of as "one-many relations," i.e., those relations which at most one term can have to a given set of others. Such is the relation of an organism to the many facets of environmental phenomena. From an asymmetrical one-many relation we can generate a one-one relation which permits of a term-for-term correlation. This we shall demonstrate is what we do when we translate the language of environmental relations to that of the unity of factors and their correlated unitary organic effect. Further detailed information on classes and relations is available from such authors as Tarski (1941); Quine (1953); Russell (1903, 1919).

The semantic dimension

Although some progress has been made in the direction of establishing a suitable language by which to discuss the semantic dimension, clarification and systematization of this language have not been comparable to that obtained in certain portions of syntactics. This is not surprising since semantics presupposes a relatively highly developed syntactics. It is impossible either to describe or discuss without language and its structure. Even to speak of the relation of a word to objects assumes, in order to refer to both, use of both a thing-language and a language about language (meta-language). Also it must be re-emphasized that, with the exception of proper names which always denote a single individual thing, most other words are class words that name a class of things, of actions, or of relations. It is therefore impossible to escape the bearing of the theory of classes and the theory of relations upon our every statement.

In semantics, as in syntactics, there has been an attempt to develop rules governing the relation of the word to the object it denotes. The first point to be clearly understood is that each of us is permitted to define his words as he chooses. Thus there is no right or no wrong definition for a particular word. Through our use of them, however, words do become at least temporarily standardized in their meaning. Such usage becomes catalogued in dictionaries and then may be said to follow the rule of common usage. However, there are very important exceptions to this rule of common usage. The most important of these exceptions is where a word, standing for something in common usage, is employed so indefinitely that dissatisfaction results from perpetuation of its use. Such a word is often an inclusive term

covering many confusions and hence must be either clarified or avoided. It is in such cases that it becomes mandatory for the scientist to analyze the words in his field in terms of the phenomena upon which they rest. He is then in a position to construct a precise definition. It must be emphasized at the outset that in science we are concerned with cognitive meaning, i.e., the expression of knowledge in terms of declarative sentences. Science is not involved with language expressing value judgments of feeling or emotion as in the case of meaning in the fine arts. We are concerned with words as the labels for things and with sentences as the labels for states of affairs. To establish the cognitive meaning of a sentence, then, is to recognize the state of affairs that it denotes and what properties it connotes; or in other words, to recognize what properties a given state of affairs must have for a sentence to apply to it. These constitute its truth-conditions.

Carnap (1936-1937, 1937), Reichenbach (1951), Rynin (1947, 1952), et al. have identified the cognitive meaning of a sentence with its truth-conditions, and thus have established both truth and meaning as a property of signs. The connection between the questions, 1) under what conditions does a sentence have meaning? and, 2) how can we find out whether it is true or false, or, in other words, how can we verify it? is pointed out by Reichenbach (1951). He indicates that "if we know what it would be for a given sentence to be true, then we would know its meaning." This verification of meaning in terms of the truth-conditions upon which a sentence is based is known as the Verifiability Criterion of Meaning or the Verifiability Principle. There have been numerous versions of the Verifiability Principle (Bridgman, 1927; Reichenbach, 1951; et al.) and it has engendered much controversy. This controversy, however, has centered chiefly around the possible infinite regress in explanations as we push further and further our quest for complete verification. Perhaps one of the most useful versions is that of Carnap (1937) who relaxes the stringency imposed by the necessity of complete verification by replacing it with varying degrees of confirmation. Confirmation then is incomplete verification and verification is completed confirmation. Carnap's differentiation allows us to include as meaningful some classes of statements which under more stringent versions of the principle would be regarded as impossible to verify. For example, certain statements about the past, statements about the future, and laws of nature can be confirmed but not verified, i.e., conditions that cannot be directly or immediately observed or pointed out, but can only be confirmed through inference. In any event, application of the Verifiability Principle should provide no serious difficulty, for its greatest usefulness is as a procedural rule for discourse, enabling and urging us to pin-point our meanings clearly and thus avoid senseless arguments. As Rynin (1952) ably states the problem, "The critical test will not consist in introspection to ascertain the presence or the absence of the feeling of comprehension, which is essentially irrelevant; what is decisive is carrying through the task of specifying truth-conditions." And further, "I do not wish to claim that no one is clear on this matter, but it is not too much to say that frequently we find ourselves mistaken when we put to the test our conviction that we understand the meaning of a statement in terms of grasping its truth-conditions—not in terms of mere words but in terms of experiences that the words refer to. For statements at least which have reference to natural and observable events, we must in the last analysis conceive the words to be replaced by events which are their meanings. When it comes then in an act of imagination, or indication, to supplanting our language by experiences, by what they mean or refer to in the realm of nature, many apparently clear and meaningful statements evaporate into confusion." Therefore, as Hospers (1954) puts it, "the value of the Verifiability Principle is like that of a purge, neither true nor false, but very effective in eliminating waste."

In the process of stating the truth-conditions, we are provided with the means that enable us to understand how to reach the meaning in statements about the oneness or unity of an aggregate. This clarifies our frequently mistaken conception of these as physical entities. The early American semanticist A. B. Johnson (Rynin, 1947) expressed this problem somewhat whimsically as follows: "Gravity, which effects so much in astronomical theories,—which has displaced Atlas, and equals him in oneness,—is still, so far as relates to its oneness, but a delusion of language. The word gravity names many interesting and important phenomena; but if, in addition to these, we look for gravity itself, we act as ignorantly as the child at the opera, who, after listening with impatience to the music, singing, and dancing, said, 'I am tired of these: I want the opera!" Likewise some of us find it difficult to consider the oneness of a forest as other than a real entity. We would attempt to confirm our statement to this effect by pointing to the trees on the hill. However, "forest" is a class word that expresses, among other things, the unity we impose upon this aggregate of these trees. That is, the unity or oneness

of a *forest* is a concept resulting from man's classification and symbolized by the word. Therefore, like gravity, when we seek to either observe or analyze this unity, we discover only individual trees. Thus such a unity is "but a delusion of language."

Another important distinction is that between the class-as-one and the class-as-many. The focal point of this distinction is that it constitutes two divergent points of view for contemplating the same constituents of the class. For example, shall we construe the class of books as one and discuss it in language of its defining properties applicable alike to all books? Or would it be more useful to think of the class of books in language that dwells upon their diversity? This is one of the most significant and most difficult of our problems. As William James (1907), in discussing the application of the pragmatic method, says: "I wish to turn its light upon the ancient problem of the 'one and the many.' I suspect that in but few of you has this problem occasioned sleepless nights, and I should not be astonished if some of you told me it had never vexed you at all. I myself have come, by long brooding over it, to consider it the most central of all philosophic problems, central because so pregnant." It seems pregnant to us because an error of judgment, so easy to make, may lead to distortion of intended meaning.

The class-as-one and the class-as-many result from two ways of defining any given class. The simplest method of defining a class is to enumerate its members, in which case we have a class by virtue of a conjunction of its terms or constituents. A class so defined is said to be extensionally defined. The other method of defining a class is to indicate how a given member is to be regarded as a member of the class. That is, by what property is it included in the class? Such a class may rest upon properties intrinsic in each member such as the common properties of members, or it may rest upon the relation of the members to some common denominator and hence rest upon extrinsic properties of the members. Such classes are said to be intensionally defined, and in this case the unity of the class is its most significant aspect.

It will be noted that the intensionally defined class rests upon properties or relations of the included members, while the extensionally defined class rests only upon the membership without reference to their properties. Thus in the intensionally defined class the meaning derivable from the properties of the class to any statement in discourse is confined to the unique set of properties or relations upon which the class is predicated. However, in the extensionally defined class, since properties do not enter the definition, they are not implied from the class word in discourse and hence must be asserted separately and the scope of their significance to the class must be enumerated with each use.

It is precisely because of this situation that the role of the extensionally defined class must be understood, for by dissociating the properties from the definition of the class the relation of diversity between the members of the class may be meaningfully discussed in terms of the class. The class thus retains its manyness rather than a unity as its significant feature and is spoken of as the class-as-many.

The plant community provides an example of the difficulty inherent in the problem of the class-as-one and the class-as-many. There are very few facts, either as properties or relations, common to all individuals of the community that are operationally significant in the relations between indviduals and their environment. Therefore the **unity** of the **community** rests mostly upon facts not relevant to the operations of the organisms and their environment. The operational facts then are pertinent to the class-as-many. Therefore the facts upon which the community as a class-as-one rests provide us with very little information that will enable us to understand the ecological relations prevailing in the community. As was the case of the forest, the language of the unity of such a community is overly impressive. This causes us to seek in vain for confirming properties to account for such unity. The maximum meaning to any statement about the community accrues when we discuss it in terms of its enumerated constituents and their individual properties, thus emphasizing the relation of diversity. This was Gleason's (1926, 1939) point in his individualistic concept of the plant community. Thus the problem of the class-as-one and the class-as-many is primarily one of language.

The pragmatic dimension

Having discussed the rules for relating words to words, and words to objects, there remains the problem of the relation of the word to the user. This is the pragmatic dimension. Because human beings design, send, and receive words, this dimension must take into account human limitations and variations thereof. Actually, therefore, it might well take into account human variations in capacity and experiences as they relate to physiological problems (limitations of perception), intellectual problems (limitations of knowledge) and psychological problems (limitations upon un-

derstanding). However, as currently developed, pragmatics tends to emphasize primarily the sources of confusion in language emanating from psychological reactions to words.[2] The realization that most of us carry prejudices as to the extent and scope of the meaning of words can well serve as the starting point of language analysis. Once this point is recognized we then can consciously proceed to employ the syntactic and semantic rules to clarify our difficulties.

We would like to proceed in this direction in presenting our theory of the environment. We therefore shall begin by presenting a synopsis of the concept of environment now current in Ecology. We hope that the reader will at least temporarily set aside his own unsuspected prejudices so as to accompany us with an open mind to a logical and semantical analysis of the concept *environment.*

A Theory of the Environment

In reviewing current concepts of environment and the uses of the word "environment," we have selected several texts on Ecology and certain papers dealing directly with the basic problems of the environment. We have reviewed these from the point of view of effective or ineffective conveyance of statement meaning. Permeating all of them, we have found elements of confusion in the display of meaning. This, we believe, results from certain prevailing confusions in syntactics and semantics which we all are guilty of in our everyday discussions of Ecology. We cannot devote space to detail a separate account of each work, so we must confine ourselves to the basic difficulties common to all. Works of the following authors were reviewed: Tansley and Chipp (1926), Braun-Blanquet (1932), Weaver and Clements (1938), Tansley (1946), Daubenmire (1947), Billings (1952), Odum (1953), and Oosting (1956).

There are several basic confusions present in all of the works reviewed. All of the authors seemed unaware that there are class levels where the problems are to be most significantly discussed. "Environment" was variously defined, but, in general, the notion of external physical phenomena impinging in some significant way upon organisms prevailed as diagnostic. However, in none of the works was there an analysis of just how a phenomenon may be identified as an environmental phenomenon. The authors seemed not to have realized that they were involved with the problem of the class-as-one and the class-as-many. All authors were plagued by the problem of what they spoke of as "interaction" and of "indirect factors" as these contribute to the complexity of the problem. In addition they were confused by the semantics of the word "factor," a word that somehow we all take for granted and assume that we understand. Very rarely does one find it either defined or consistently used.

Some authors made a distinction between environment and habitat. They appear to have used "environment" in the universal sense and "habitat" in the existential sense. However, habitat was considered as the place (in addition to the conditions) where a group of organisms lives. "Environment" was employed as a general term for the sum of all habitats and habitat conditions. We find this particular distinction of words inappropriate.

Analysis of the concept environment

We come now to the point where we wish to clarify our understanding of the concept *environment* as employed in Ecology. First, it is essential that we realize that in such an investigation all that we have to work with empirically are: 1) organism, 2) physical phenomena that enter a significant relation with the organism, 3) the empirical relations between the phenomena and the organism either singly or in various combinations. All else that has been traditionally included in environment is either intellectual organization, interpretation, or accessory aggregation.

With these as our facts, let us now proceed to analyse the concept *environment* (Fig. 2). The first step is the realization that 1) "environment" is a class word and 2) the concept is organism-directed. **Environmental phenomena** in the universal sense are all of that class of phenomena which have or may have an operational relation with any organism. This is the primitive proposition of our argument. There may be other phenomena present that do not enter a reaction system; these are not environmental phenomena. The sum of the empirical relations between the various environmental phenomena and any individual organism constitutes a unity which is **the environmental relation** of that organism. The class of phenomena determined by this environmental relation, i.e., only those phenomena that actually enter a relation with a particular organism, constitutes **the environmen**[illegible] of that organism. Because it is concerned only with such phenomena as are immediately and directly operationally significant

[2] General Semantics, under the leadership of Koryzbski (1933), is likewise concerned primarily with the psychological impact of language upon senders and receivers. Due to its popularization by such writers as Hayakawa (1954), the general public often tends to associate semantics with much of what is here relegated to the pragmatic dimension.

to a given organism, we speak of it as the **"operational environment"** of that organism. We should make it clear at this point that our use of the term "operational environment" is not to be confused with "operationalism" of Bridgman (1927).

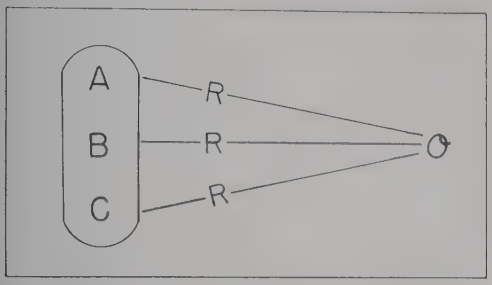

FIG. 2. Diagrammatic presentation of the concepts *Environment* and *Environmental Relation.*

All unused phenomena that are in a condition to be operationally employed by this organism we speak of as its **"potential environment."** Thus "environment" *per se* is synonymous with "operational environment." It must be understood that potential environment is only capable of becoming operational and hence is not yet environment.

Operational Environment—It must be continually emphasized that the operational environment is always the environment of a particular individual organism. There is no aspect of environment, in the sense of actively operating phenomena, that is not related to individual organisms. Even in cases where one organism is an environmental phenomenon of another organism, the viewpoint is always toward one of the organisms at a time. There are no phenomena operationally significant to such aggregates of organisms as species, stands, communities, associations, or floras except as summations or as logical products of phenomena operationally significant to the included or associated individuals. We shall elaborate this point later. This, we think, makes it clear that so far as operational phenomena fall under the concept *environment,* such a concept must be organism-directed and directed toward an individual organism if our language is to be freed from the difficulties imposed by the abstract unities of the aggregate level. It is easy to translate to aggregate phenomena after the environmental relations of the individuals are established and understood.

We may therefore conclude that *environment* is organism-directed toward an individual organism. If we develop a concept of the environment that is not only organism-directed, but also directed toward one particular organism, how may such a viewpoint be confirmed as being adequate to the task? This requires an example. Water is only water until we introduce an organism. At that moment it becomes the environment of the introduced organisms. If we place an organism in a body of water we have an example of water as an environment of the organism. If we now remove the organism, this water is no longer a part of the environment of this organism. If we now place several organisms in the body of the water and remove them one at a time, the water ceases to be the environment of each organism in turn as it is removed. It follows that a given body of water as it provides an aquatic environment for a group of organisms constitutes a separate environmental phenomenon relative to each individual organism regardless of kind. A similar demonstration can be set up to confirm the meaning of similar statements as they may pertain to any and every environmental phenomenon. We shall see later that the confirmation of facts relative to aggregates of organisms involves logical transformation or deduction from statements of phenomena observable for individuals.

If we define "environment" relative to each organism, what point in the life cycle do we select to draw our definition? Since the individual organism varies in its environmental demands throughout its ontogeny, to select any given time would of necessity leave out some significant aspect of its environmental relations. Hence these facts would not be represented in any meaning the word "environment" would have as applied in a statement relative to this organism. Obviously the way around this difficulty is to bring a concept of time into our definition of evironment. Time can only be confirmed in terms of the duration of some event; it cannot be confirmed independently. Such is the time with which we are concerned in our problem. Since we must define "environment" relative to particular organisms, to include all of the environmental relations of any organism we must define it to include the entire life cycle of that organism. Thus the life span of the organism is the duration time of its environment. The confirmation of this statement is simple. Remove the organism and the essential time reference for the concept *environment* is lacking. Replace the organism and we again have an environment. Throughout the time the organism is living we can speak of the phenomena that significantly impinge upon it as its environment. When the organism dies this relation ceases. We may con-

clude then that operational environment is organism-timed.

Throughout the ontogeny of the organism, its environmental demands differ. This is not a haphazard relationship. It is very orderly and the order is correlated with the requirements of the ontogenetic stage of the organism. Thus we may say that the environmental relation is ordered by the ontogeny of the organism. It follows that what constitutes the class environment must include all phenomena demanded by this ordered sequence of relations. This however is not entirely a one-way relation for, in turn, some aspects of the ontogeny of the organism are ordered by sequential events in the environment. It must not be implied that the phrase "ordered-by" indicates that the environmental sequence is controlled by the organism. All that is meant is that the sequence of the demands of the plant are dictated by the needs inherent in the ontogenetic cycle. In some cases these follow a sequence controlled by ontogeny. In others they follow a sequence controlled by the environmental change. In either case there is a correlation between ontogeny and environment, and for our purposes it is most useful to think of them from the point of view of the organism. These statements may readily be confirmed by the same set of phenomena. If we germinate seed near the minimum temperature for germination, we will find little or no growth of the seedling until the temperature is raised. Then growth will be stimulated. For many plants a further increase in temperature is necessary for flowering. Here is a correlation between ontogenetic development and environmental change in which the capacity of the organism to respond is a significant property of the organism and often is genetically controlled.

We have next to consider area or space of the operational environment. This is contingent upon precisely how much of any given environmental phenomenon is to be considered the environment of the organism. If we consider a small aquatic plant in a large body of water and as we approach it we try to determine just where water, as only water, ends, and water, as also the direct environment of the plant, begins, we will find ourselves singularly lacking in criteria with which to judge this fact. The only relation that we can positively confirm will be to that water, and only that water, which directly affects the reaction systems of the plant in its metabolism or that which when in direct contact buoys the plant. We will be forced to adopt an operational point of view and speak of an operational environment as those phenomena that actually and directly impinge upon the organism during its life cycle as ordered by the ontogenetic sequence of the organism. It will be impossible to confirm any statement to the effect that a molecule of water even a millimeter away from the plant is a significant fact in the metabolic environment of the plant or buoys the plant directly. Such a statement would be a meaningless statement. The water is significant only at such points where it presence or absence makes a significant difference to the plant. Where such a difference occurs the water is operationally significant. It must follow that the space of the operational environment is coextensive with the operation. Therefore we may conclude that environment is organism-spaced.

It thus seems clear that as we allow these facts to influence our concepts of environment we will have a concept stripped of all extraneous matter and limited to those phenomena that acutally enter a reaction system of the organism or otherwise make some differences to the organism sometime during its life cycle. This is all that we can confirm; it is all that is significant to any given organism in question. Anything that we cannot confirm directly through test or observation or indirectly through inference as playing a role in the life of the organism, we cannot confirm as constituting a part of its operational environment.

Thus we arrive at the following definition: *The environment of any organism is the class composed of the sum of those phenomena that enter a reaction system of the organism or otherwise directly impinge upon it to affect its mode of life at any time throughout its life cycle as ordered by the demands of the ontogeny of the organism or as ordered by any other condition of the organism that alters its environmental demands.* This definition expresses operationally a time-space-organism concept of environment whose constitutents form a class. Furthermore the truth-conditions upon which it rests are all at least theoretically confirmable through observation, experiment, or logical inference. Through the analytical methods of semantics these truth-conditions may serve to establish statement meaning. Since the potential environment cannot be directly confirmed but is confirmable only through predictable inference from an operational case involving like environmental phenomena, the only sense in which the word "environment" can carry direct confirmable meaning is when applied to an operational environment. Therefore when we employ the word "environment" without qualification it can only mean operational environment as referring to those environmental phenomena that actually enter or have entered a reaction. Where we specify "opera-

tional environment" we do so for emphasis only. When we speak then of the role of environmental phenomena without reference to any operation, or speak of any sense of conditioning environmental phenomena or of selective potential and similar concepts we must specify potential environment to avoid ambiguity.

It will be noted that our definition does not allude to the idea of encircling or surrounding inherent in the etymology of the word "environment." The etymology of the word must be regarded as wholly secondary to its meaning. The concept *to encircle or surround something,* implying a spatial relation, has no value to us in our usage, although many users seem to add this idea to their discussion of environment. It is of historical interest only.

The class environment.—We must now determine with what kind of a class we are dealing. Early in our discussion we called attention to the fact that "environment" is a class word referring to a class of phenomena that constitute the environment. When we employ the word "environment" we often introduce confusion into our language because it refers both to the class as defined intensionally and to the class as defined extensionally. When we speak from the intensional point of view, we may not realize that only defining properties are significant to statement meaning, and we discuss other properties as though they were significant. About all that the environmental phenomena have in common is that they impinge in some significant way upon the organism. This, we pointed out, is the defining property of the class environment; it will be noted that it is based upon extrinsic relational properties of the constituents of the class. More significant to "environment" as we employ it, however, is the *way* in which each phenomenon impinges upon the organism, and the fact that each phenomenon impinges differently. This is a signal that we should be viewing environment as a class-as-many. We are concerned with a class of phenomena whose unity functions only to focus attention toward a common objective in discourse. What is important is the different significance of each phenomenon to this common objective. Such differences are not included in the scope of meaning of any statement relative to the class-as-one. Thus it should be clear that the viewpoint demanded of us here is that of the class-as-many, i.e., the same class, but seen from a different viewpoint. Hence, the greatest value to ecological interpretion is obtained by discussing environmental phenomena in their separate and related impingements upon an organism.

If one treats the environment as a class-as-one, complexity upon complexity begins to accrue to the class. If we then include such matters as "indirect factors" and environmental interaction, attention becomes focused upon them and they appear to be the most characteristic features of environment. Attention is thus directed away from the relation to organism.

Relative to *environment,* the class-as-one serves only to establish its defining properties. Understanding of the role of the constituents of the class will entail the detailed study of each phenomenon of the environment in every aspect of its relation to organism. The key to the problem is a reaction by the organism directly to the phenomenon. Any study must begin here; here is the relation around which conclusions must be drawn, and herein rests the confirmation of any statement that can be made about it.

The Environmental Relation

We must now make a clear distinction between environment and the environmental relation (Fig. 2). We have pointed out that the class of phenomena that constitutes the environment is predicated upon each such phenomenon, being operationally significant to an organism usually each in some different way. Each such operation, with an environmental phenomenon as its predecessor and the organism as its successor, constitutes a relation between this environmental phenomenon and the organism. The logical sum of all such relations with the organism constitutes the class of environmental relations of that organism. Conversely the organism may be involved in some significant relation with the environment. It should be clear that this latter relation is very different from the former. Since it is operationally significant to the conditioning of some potential environment rather than being immediatetly and directly significant to the organism, it does not qualify under the defining properties of "environment." As was pointed out in our introduction, such a relation is asymmetrical and only that part of it wherein an environmental phenomenon impinges upon an organism qualifies as significant to what we here speak of as the environmental relation. In such asymmetrical relations the direction of the relation from predecessor to successor is always significant. Hence any other relation or class of relations whose successor or counter-domain is the environment, or is any fact in the history of environment, regardless of what the domain of the relation may be, belongs to a different relational field. It follows that no fact in a sequence or progressional series of different

asymmetrical relations leading step by step to the conditioning of the environment is a significant environmental relation of an organism. No fact in these prior relations other than the final conditioned environmental phenomenon can be construed as directly operationally significant to the organism.

When we analyse the environmental relations of any organism to the extent that they are known, we find that the environmental phenomena involved are precisely those that account for the selection of the organism by the environment. We may thus conclude that the set of environmental relations constitutes the relation of natural selection. Hence this set of facts constitutes a common focal point for the Ecology, Taxonomy, Genetics, and Physiology of plants in nature.

Environmental Factors

We have called attention to the fact that confusion reigns in the handling of the concept *factor* in the current literature. "Factor" is a word whose usage well illustrates the pragmatic dimension of language. We all use the word so loosely, so frequently, and with so much feeling of comprehension that we never question its meaning. If one is questioned as to his usage, an antagonism to the question may be raised which promotes the answer, "Of course, I know what it means." Yet the current literature indicates that we apparently have little notion of what the truth-conditions are in any given case.

Actually we employ the concept *factor* as an abstraction for unifying **in language** a one-many relation by reducing it to a one-one relation in order that we may grasp the significance of correlations between environmental phenomena and biological processes. For example, any part or all of those environmental phenomena presumed to be related to photosynthesis are abstracted to unity. They then serve as the unique predecessor of a relation whose successor is photosynthesis. The abstract environmental phenomena may then be spoken of as a "factor." It will be noted that the term "photosynthesis" is also a unitary expression for a complex system of reactions. The term "factor," however, refers only to environmental phenomena as organized in language and always implies a one-one relation. Thus we may define "factor" *as a concept that expresses unitarily the one-several environmental phenomena related to a given organic effect.* The confirmation of any statement regarding the relation of factors must be made at the empirical level of the environmental phenomena concerned. It should be made clear, however, that intellectual unification does not imply an interaction on the empirical level. What we may regard as two or more phenomena related to a single effect constitute, when reduced to unitary simplicity, a single factor. This tends to reduce to nonsense much of what has been said about single factors not being limiting and in fact renders meaningless all discussion about the interaction of factors significant to environment.

Thus we see that environmental factors are constituted of environmental phenomena. Like environment, factor is organism-directed, and may be directed toward effects or processes within the organism singled out for observation. Hence it may be one environmental phenomenon or any unitary combination of them. It may be toward one process or effect or any unitary combination of processes and effects in the organism. For example, in figure 3, A may represent water as it is significantly related to the process of transpiration, w, in organism, O, and C may be temperature as it is related to germination, y. Water and temperature may thus be separately considered as factors. However, we may also refer to the combined relation of A as some aspect of water, B as certain wave lengths of light, and C as a given amount of heat as they significantly relate to the common process photosynthesis, x. The abstraction of (ABC) R x could then be considered relative to their sources as the climatic factor of photosynthesis. Also D as calcium ions in the soil solution, E, as soil oxygen, may be combined unitarily as an edaphic factor of ontogeny which in itself is an abstraction of the processes of germination, y, and growth, z. This relation may be expressed: (DE) R (yz). Therefore, in each case we have reduced the many to the one, and established through abstraction the one-one relation, i.e., factor to organic effect. Often, as knowledge advances, what we have regarded as a simple environmental phenomenon may better have been discussed as a factor since further analysis discloses it to be more complex than was originally supposed.

It is also necessary to point out that an element of confusion may inadverently come into our contemplation of these relations if we are not aware that the concept *factor* in its elasticity may extend to embrace the sum of the phenomena that constitute operational environment (A, B, C, D, E) which we may wish to think of as one. When all environmental phenomena are abstracted to one, whether we relate it to a single organic reaction (w), to any combination of them (x, y, z), or to the entire organism (O), "factor" and "environment" as words become synonymous.

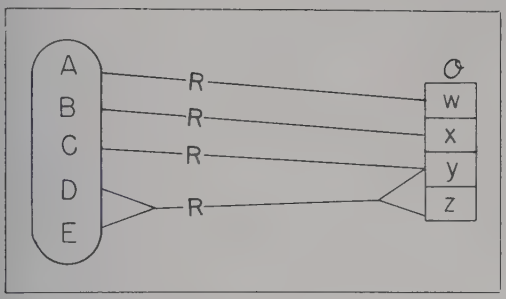

FIG. 3. Diagrammatic presentation of the concept *factor* (see text for explanation).

This raises no problems where it is understood. Actually the word "factor" is unnecessary because everything can be stated by enumerating environmental phenomena and their relations. However, we retain the word "factor" because it is a convenient language device in pointing out a one-one relation when interrelated phenomena stand in relation to a single effect.

NON-OPERATIONAL PHENOMENA

But what of the remainder of the phenomena which we have traditionally regarded as constituting the environment? These fall into two classes of phenomena: 1) those that are in a state capable of entering into a reaction with an organism but have not yet been called upon to do so—we refer these to the potential environment; 2) those phenomena that are not directly usable by the organism, including those that must be altered before they will be available to an organism—we place these in the class non-environment.

Potential environment

The operational environment with respect to most environmental phenomena becomes used up in the operation. What is left of like phenomena is the potential environment of this or like organisms, or of other organisms employing this set of phenomena. Operational environment, both from the point of view of its unity in the class-as-one and its diversity in the class-as-many, establishes the defining properties of "potential environment." These defining properties provide a concept of the kind of phenomena that make up the potential environment. Thus through inference the concept *potential environment* is derived from operational environment. We can now inferentially extend its use to all like organisms. Also through a summation of potential environments of the different kinds of organisms we can extend the concept as far as we may need. Since operational environments constitute the sources of meaning of potential environment so must we return to the operational environment of individuals as the source of confirmation of any statement we may wish to make about the role of potential environment to a potential relation.

What may be a part of the potential environment of one kind of organism may not be part of the potential environment of another kind of organism, and the role of a given phenomenon in one organism may differ from its role in another. Or the role may vary with ontogenetic stages for the same organism under different sets of environmental conditions. We should not assume that either any conditioning agent or any conditioning process is the operational or the potential environment of the organism. The conditioning agent is a fact in the history of the environment that we shall discuss presently. Potential environment must be construed as being already in the proper state for the reaction it is to perform.

Non-environment

Because they cannot be confirmed as immediately and directly entering a reaction with an organism, all other phenomena traditionally associated with environment, even though near or surrounding the organism, must be excluded from the concept *environment*. These include all that have been included under the terms "indirect factors" and "interaction" as well as those to which the organism may be indifferent.

The problems of indirect factors and those of the interaction of environmental phenomena, if not one and the same, are so closely related as to be scarcely distinguishable. At least so far as the environment is concerned, these problems resolve themselves into the same difficulties. The common denominator between them is that both function to condition a phenomenon of the environment to which an organism then reacts. Important as this is to the ecosystem, the only reaction that we get from an organism is to an already conditioned phenomenon. The state of a phenomenon prior to its conditioning is outside the scope of the concept *operational environment*, and hence also outside the scope of the concept *potential environment*. It does not have the defining properties of an environmental phenomenon. This may seem to some to rest upon trivial distinctions, but we are convinced that this is the precise boundary between clarity and confusion in the problems of the environment. Such phe-

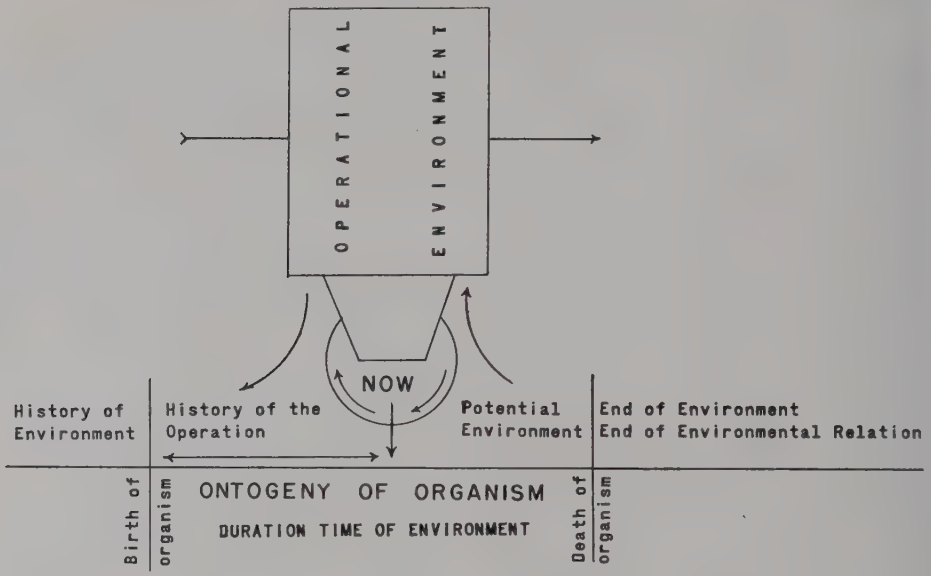

FIG. 4. Diagrammatic summary of the theory of the environment.

nomena constitute facts in the history of the environment. An event of history is of importance because of its place in a sequence of events; each step from predecessor to successor event constitutes a relational field of an asymmetrical relation. Further, each step being a different relation and involving different related phenomena, it would constitute a confusion of logical types to reduce all such steps to a two-term relation from any given predecessor (except the last) to the final successor. Therefore, it is logically inadmissable. It follows that we must reject the implication that such chains constitute a unitary event playing a significant role in the environmental relation even though the steps are very important to the ecosystem.

There is also a philosophical reason for removing indirect factors from the concept *environment*. To introduce indirect factors into causal relations within the environment is to introduce an infinite regress into the system of explanation. Every cause has in turn itself a cause which becomes an indirect cause of the most recent effect. The regress is toward the limbo of ultimate cause along an infinitely reticulating path; for this we have neither finite description nor finite explanation. The only reaction the organism makes is directly with the phenomenon of the environment as it finds it at the moment of the reaction. This is a finite phenomenon and the reaction is a finite reaction. What we are dealing with in indirect relations is environmental history which is equally important to Ecology and whose understanding is often necessary. To include such relations in environment is to confuse environment with its history. This in no sense diminishes the importance of these facts; it only places them in a context in which they are important and removes them from a context in which they can only serve to confuse.

Although the environmental relation follows in sequence from the events of environmental history, the break between the two is clear. As the environmental relation proceeds, it generates a history of itself. A glance at Figure 4 will make clear that we must not confuse the history of the environment with the history of the environmental relation. The history of the environmental relation is coincident in time and sequence with the ontogeny of the organism from its inception as an organism until a moment of time that we may speak of as "now." It is the story of the sequence of the relation of environment and organism.

Figure 4 also is a summary diagram of our theory of environment as it involves: 1) the operational environment as ordered by the ontogeny of an organism, which is also its time or sequence reference, 2) the potential environment as capable of becoming the operational environment, and 3) the distinction between history of the environment and history of the environmental relation. We have not included in the diagram any effect

of the organism on the unused potential environment. This would be a fact in the history of the environment.

Potential Environment and Aggregate Levels

We must approach the problem of the environmental relations at the aggregate levels with full awareness that all of our facts stem from individual organisms and their individual environmental relations (Fig. 5). From such facts we can by inference gain a concept of the potential environments available to an aggregate of individuals. *Potential environment,* as a concept, is an intellectual organization of facts. In the intellectual organization of environmental phenomena where the concepts are directed toward classes of individuals such as species populations or communities, the summation of the potential environments involved is as far as we can go. We can sum to whatever floristic or geographic extent we may find necessary.

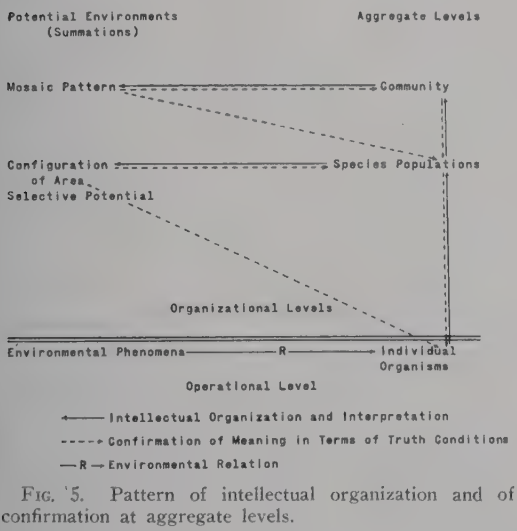

Fig. 5. Pattern of intellectual organization and of confirmation at aggregate levels.

In the intellectual organization of the aggregates of individuals such as the plant community, we usually define the species populations at one level and aggregate those associated populations in accordance with some concept of geographic or floristic homogeneity to constitute the community at a higher level. These organization levels then serve as an organization system whereby we may describe and explain the relations between environmental phenomena and organisms, or relations between organisms that we may discover at the empirical level. For example, such facts as physiological reactions are all best explained at the empirical level of an individual organism. We may, however, be able to employ certain facts descriptively at higher aggregate levels through summation. On the other hand the phenomena of genetics provide much that is most clearly described in terms of the population. But it should be clear that the operations all happen at the level of individuals. Even pollination and gene transfer are genetically significant primarily because the operation is one performed by individuals. Facts about ecological diversity between individuals are best described in terms of the patterning of the community. Explanations are always at the empirical levels of individuals.

The fact that operational environment is organism-directed means that our organization of a concept of environment at higher levels must also be organism-directed. Therefore, there is no independent organization system that gives us a hierarchy of operationally significant environmental phenomena other than the simple facts of singular and plural as they relate to the environments of the included individuals. This provides us with the key to confirmation since we must return to basic empirical phenomena either directly or by way of successively lower levels of the hierarchy of the system of organisms (Fig. 5).

The facts of natural selection as they may involve a homogeneous species population could even be discussed in terms of explanation at the level of species population without distortion of meaning because what can be said of an individual can be said of such a class. However, when we come to the community, explanation must return to the empirical level because natural selection operates differently for the different members of the community.

With respect to configuration of area and mosaic pattern, it may be seen that at the species population level patterns relate to the facts of natural selection and the variability of the population as it becomes elaborated over the area of potential environments. At the community level our problem is more complex. If we are concerned only with mapping the pattern, a simple summation of constituents is all that is involved, just as in fitting together the pieces of a jig-saw puzzle. If we wish explanation in terms of environmental relations, we are confronted by a complex system of logical products. The overlap or the logical product will be wherever two or more organisms occur in the same environmental complex due to their having the same environmental relations. These will constitute one element of the explanation. There may be any number of different situations of this type. Another element will be

where two or more organisms occur in the same environmental complex because they make different or partially different demands on the environment. Such situations may present many variations in degree. When such selective patterns as the above are superimposed over a highly complex environmental mosaic, we see displayed the complicated nature of the problem of the community and its environmental relations. However, with this display, we also see clearly where we must turn to investigate or to confirm any fact of this problem. We are thereby directed to return to the individual organism either as an example of its species or as an example of a variant of its species. This latter case includes the problem of the ecotype as clarified by Kruckeberg (1951). Ecotypes, when not coextensive with a taxonomic class, must be treated from the point of view of the class-as-many. Only in this way can we explain how a given individual may be a member of two different ecotypes whose geographic ranges traverse one another but are not coextensive.

It should be clear that if at all aggregate levels our problem is one of inference, it follows that when we attempt explanations in terms of empirical relations which we presume operate at these levels, the resulting confusion is intellectual rather than in the facts available at the empirical level. The views presented here may help to illuminate further the problem of environment and the aggregate levels treated by Whittaker (1954), by making clear the range of significance to which any given set of facts may pertain. It also may aid in clarifying the significant levels and their limits to which Major (1951) might direct his analysis of the ecosystem.

Classification of Environmental Phenomena

The classification of the phenomena that enter the environmental relation is a very troublesome subject. As far as we can discover, it has never been very successfully treated and we certainly are not proposing to undertake it here. However, a few remarks on the requirements of such a system are in order. There are many ways in which any set of phenomena may be classified. Classifications are all man-made. However, when they reflect relations between natural phenomena we speak of them as a natural classification. There is nothing in the subject matter that demands that we classify or that we confine ourselves to one system of classification. Since the need for classification is dictated by utility, perhaps more than one system may be desirable.

The system of classification most commonly employed at present, whereby environmental phenomena are classified as edaphic, climatic, and biotic, is based upon source without very much attention being given to how useful the classes thus derived may be. The difficulty with this classification is that source of the phenomenon is of little or no significance to the operation the phenomenon performs. For instance, oxygen both in the soil solution and in the atmosphere performs a function. It is needed differently in both places. The origin of the oxygen is not significant to the operation. A similar case may be made for water. Such classes of phenomena as rainfall, temperature, evaporation rate, soil texture, and parent material play little direct role in the environmental relations of organisms.

In Ecology we are chiefly concerned with the relations of environment or environmental phenomena to organism. It would seem then that a more useful classification would be one that reflected something of this relation and one whose classes would be useful in generalization. Since these relations are physiological, one would presume that a physiological classification would accomplish this. However, a physiological classification may not be very easy to establish. Unless we can further our generalizations with the classes generated in such a system, there is little point in such classification.

Another view of classification might be directed toward phenomena significant to natural selection. This of course would involve the potential environment in the universal sense. The classification would have to be designed around the selective problems of an individual organism since it is always an individual that is actually selected. Then such phenomena as selectively significant factors and permissively significant factors would play a discriminative role in the system. Rejective or inhibitive factors would also play a role in such a classification even though no rejective phenomenon ever selected an organism. However, since they reject they are operationally significant when doing so. Rejective factors belong to that infinite class of explanations which accounts for the millions of organisms not being where they are not. Therefore they need to be very carefully scrutinized in each case in order that we do not introduce an uncontrollable trivial element in the system. Rejective factors need to be thought of in terms of operations that actually function to eliminate an organism from the community only at such time as an organism may present itself.

Some thought might be given to a classification based upon energy and substance. This, however,

would call for careful attention to language, for when we move into discussions of energy relations, everything that we now know as a thing will become a space-like event and processes will become time-like events. Such a classification would require an appropriate language to express these events and to translate them to the realm of sense impressions.

Conclusions

The most pertinent question that could be asked at this point is, "What difference does all of this make?" Our answer follows.

With the methods of the three dimensions of language analysis we have stripped the concept *environment* of all but those truth-conditions that we can confirm as directly entering a reaction with an organism, and thereby we have made clear the sources of its meaning. In order to be classed as an environmental phenomenon a given phenomenon must, 1) be operationally significant to an organism, 2) be directly effective at some time during the life of the organism, 3) be effective as to sequence as ordered by the ontogeny of the organism. We thus have a concept of environment that is organism-directed, organism-timed, organism-ordered, and organism-spaced. The sum of such phenomena as actually enter an operation with an organism constitutes the operational environment of that organism. The operational environment provides the class concept or defining properties of a class called by us "potential environment" which includes all unused phenomena of the same kinds as were included in operational environment.

We have removed from the concept *environment* all of the facts of environmental interaction *per se* and all indirect factors as well as all surrounding phenomena that are in no way directly significant to any operation with the organism. In eliminating such extraneous matter we have removed much of the frustrating complexity of environment. We have also reduced the operational problems to those of individuals and have thereby greatly clarified the perspective of possible experimental investigation within the disciplines of physiology. We have furthermore pointed out the logical hazards of introducing an infinite regress into our system of explanation as is done by insisting on employing indirect factors as being of significance to causal relations. Rather we should confine ourselves to direct factors since they are the only factors to which a direct response by the organism can be confirmed.

Statements about environmental relations at aggregate levels reached through inference may now be confirmed by tracing these relations to their individual organism sources, rather than tracing them through a complex system of interaction or through sources confused with environmental history. Unless environmental relations can be so traced to their organism sources, any statement expressing them is a biologically meaningless statement.

Classification of environmental phenomena should reflect some aspect of the operational relations of the phenomena to organisms. Physiology, natural selection, and energy relations are fields of operational significance towards which we direct attention. At the moment we regard natural selection as providing a workable and highly useful basis for such a classification.

Finally we wish to point out that we present this subject knowing full well that this investigation is far from complete. We only hope that we have pointed the way to a clearer understanding of a much confused subject. In closing we return to our introductory quotation from Einstein, who called attention to the fact that theoretical knowledge is "hypothetical, never completely final, always subject to question and doubt."

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STUDIES IN HALOPHYTES

II. ANALYTIC DATA ON THE MINERAL CONSTITUENTS OF THREE SPECIES OF *ATRIPLEX* AND THEIR ACCOMPANYING SOILS IN AUSTRALIA

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Introduction

The high ash content of the leaves of species of *Atriplex* has for some time been regarded with interest by botanists, and the ability of these plants to accumulate large quantities of sodium chloride has led to the development of various hypotheses on the function of the salt in the leaves. These hypotheses will not be dealt with here; this paper is intended only to present analytical data for field plants and their associated soils. In a later paper (Ashby and Beadle) the results of experimental work designed to verify or refute certain aspects of halophyte nutrition are presented; for comparative purposes the analyses of field samples are essential.

The writers are indebted to Messrs. D. Adamson and J. James for providing material from Condobolin and Hay, and to Dr. R. N. Robertson (C.S.I.R.O.), Dr. W. C. Ashby (Fulbright Scholar at The University of Sydney, now at the University of Chicago) for helpful discussions.

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Materials

Three species have been selected for study; these three (*Atriplex vesicaria, A. nummularia,* and *A. inflata*) are the most common in the semi-arid country, and they are also the most important economically. The habit and approximate distribution of these has been mentioned previously (Beadle 1952). The plants analysed were collected in widely separated localities (Bourke, Condobolin and Hay) situated on the eastern fringe of the area of the species where the average rainfall is 14 to 16 inches per annum, and in the Broken Hill district where the mean annual rainfall is 10 inches. The plants therefore come from the wettest and the driest sites in New South Wales in which these species occur. One site (Salt Hole Creek, near Broken Hill) represents the most saline locality in which *Atriplex* has been recorded by the writers.

Techniques

Field sampling

Leaves were collected in the field during the cooler months only. Mature, living (but not senescent) leaves were gathered in each case. The leaves were dried in the field in paper packets and taken to Sydney for analysis. Soil samples were collected at the same time; samples were taken from under the bushes from which leaves were collected and to a depth of (usually) 12 inches, which depth includes most of the root system of the plants (except *A. nummularia*). Surface (0-3 inches) and subsurface (6-12 inches) samples were collected in almost every case.

Ash was estimated by dry combustion at a temperature not exceeding 550°C. After weighing, the ash was dissolved in dilute HCl and filtered. Silica was present in very low concentration—2% of the ash, and was not estimated quantitatively (2% is probably a high estimate since some of the residue was probably dust from the leaf surfaces). The acid solution was used for the estimation of sodium, potassium, calcium, magnesium, phosphate and sulphate.

Sodium, potassium, and calicum were estimated quantitatively using an Eel flame photometer.

Magnesium was estimated only qualitatively by precipitation as magnesium ammonium phosphate. Since, the amount of magnesium was invariably low and represented only a small fraction of the total cations, quantitative estimations were omitted.

Phosphate was estimated by the molybdophosphate reduction technique using stannous chloride as a reducing agent (Diagnostic Techniques, 1948). The colours were read on a Unicam spectrophotometer, at λ 6750 Å.

Total nitrogen was estimated on duplicate samples by the Kjeldahl technique.

Chloride was estimated on water extract of the leaves. These were oven (60°C) dried, weighed, and boiled in distilled water for a minimum period of 1½ hours. The chloride was precipitated with $AgNO_3$ and the excess of the latter was back-titrated with NH_4 CNS using ferric alum as an indicator.

Organic carbon was estimated by the Walkeley-Black method as described by Piper (1942).

For sulphate, qualitative tests only were made on the ash solutions and on soil extracts (1:5 soil water ratio).

The pH was estimated colorimetrically using the separate indicators brom-cresol purple and phenol red. The values are correct to 0.3 pH unit.

Presentation of Data

Since 25 plant samples and two horizons of 11 soils were analysed it has been thought convenient to group data as follows:

For plant material, means have been taken for plants growing on soils from the same locality. Standard deviations are given. This appeared justifiable in view of the similarity of the results.

For the soils, although the two horizons of each were analysed separately, the figures have been averaged to give a mean value of the various constituents in the top 12 inches of soil. The figures quoted probably give a reasonable estimate of the composition of the soil explored by saltbush roots (except for *A. nummularia* whose root-system penetrates to a depth of several feet). Actually the 2 horizons of all the soils investigated were usually markedly different in the various constituents; furthermore previous experience has shown that sampling the same soil at different times of the year gives quite different results for the most soluble constituents. This is caused firstly by the washing downward of soluble ions during rains and secondly by the addition of salts to the soil surface when leaves fall from the plants during dry periods.

Data, both for leaves and soils, are expressed as percentages of the oven-dried (105°C) material.

Results

Plants

The most striking features of the analyses of the leaves are that the percentage ash and percentage chloride are very alike (Table I), irrespective of species and of locality and soil. A similar observation has been made by Wood (1925).

Calcium is invariably much lower than the monovalent ions and makes up about 10% of the total cations in all cases. Magnesium, which has not been estimated quantitatively occurs in all leaves examined in much lower concentrations than calcium. Indeed it was difficult to obtain reliable positive qualitative tests for magnesium and for this reason no attention has been paid to this element.

In all cases the percentage sodium exceeds the percentage potassium. The relative proportions of these two ions, however, vary considerably; further discussion of this point will be reserved until the soil characters have been discussed.

As far as the anions are concerned, chloride dominates in all cases. Sulphate, though present in all cases, occurs at relatively low levels—so low in comparison with the chloride, that quantitative estimations are hardly worth while.

Total phosphorus and total nitrogen are both

TABLE I. Analyses of the leaves of field plants of three species of *Atriplex* from various localities in western New South Wales. Data expressed as % of oven-dried (105°C) leaves

Species and Locality	Soil No. (See Table 2)	No. of observations	ash %	Ca %	Na %	K %	Cl %	P %	N %	Cl m. e. %	Na + K m. e. %
A. vesicaria Hay	1; 2; 3	4	30.8±4.2	1.2 ±0.3	6.5±1.6	3.9±1.2	12.6	0.15±0.03	2.5	0.35	0.38
A. vesicaria Bourke	4; 5	6	31.6±0.5	1.1 ±0.31	7.1±0.5	2.3±0.3	11.2± 1.1	0.15±0.02	...	0.32	0.37
*A. vesicaria** Condobolin	6; 7	2	24.4	0.76	5.2	2.2	9.6	0.14	...	0.27	0.28
A. vesicaria Broken Hill District	9	3	32.3±4.3	0.81±0.19	7.2±1.8	2.0±0.8	13.6	0.12±0.02	3.1	0.38	0.36
A. vesicaria Broken Hill District	10; 11	4	33.4±1.3	1.2 ±0.2	7.1±0.4	2.3±0.7	13.0± 0.3	0.14±0.03	...	0.38	0.37
A. nummularia Hay	1	1	35.0	0.75	7.9	3.0	12.9	0.14	2.2	0.36	0.42
*A. nummularia** Condobolin	6	1	29.1	0.52	4.5	2.6	9.9	0.06	2.7	0.28	0.26
A. nummularia Broken Hill District	8	1	34.4	0.31	6.3	5.6	12.3	0.17	3.3	0.35	0.42
A. inflata Hay	3	1	31.8	0.56	7.4	1.5	12.4	0.18	2.7	0.35	0.36
A. inflata Broken Hill District	9	2	38.2	1.9	6.3	3.3	.....	.....	.....	.....	0.36

*Cultivated plants. *A. vesicaria* does not occur naturally at Condobolin.

high; the level of phosphate in the leaf is of the same order as that of mesophytes, while the level of nitrogen is similar to that in the herbaceous nitrogen-fixing legumes. This last point has been noted previously with reference to the value of saltbushes as forage plants by Turner (1891) and Morrison (1949).

The high values for the monovalent ions are of particular interest, particularly the values for sodium which are largely responsible for the high ash-content of the leaves. The fact that the sum of the ionic equivalents equate with the ionic equivalent of chloride indicates that the cations are balanced by chloride. Further support is given to this by the observation that the ashes of saltbushes scarcely effervesce when moistened with acid, apparently because the ash consists chiefly of chlorides.

Soils

Table II gives details of certain properties of soils supporting saltbushes. These soils have been selected to include all the common soil groups which support *Atriplex* in abundance (frequently as the dominant).

Although the soils have certain properties in common, for example a low organic content, a low phosphorus level (in comparison with analagous soils from other parts of the world e.g., certain soils from Arizona analysed by Fuller and McGeorge, 1951), and similar textures, they show very great differences in the constituents in which we are interested as far as *Artriplex* is concerned. Most surprising is the low choloride level in most of these soils; in one case only (Salt Hole Creek) does the salinity reach an exceptionally high value. Furthermore in this soil alone does the water soluble sodium reach high levels. Water soluble potassium in some cases is very low, and in most cases is very much less than the water soluble sodium. Soluble calcium likewise varies considerably, having both high and low values, sometimes exceeding the value for potassium, but in every case lower than the water soluble sodium.

The exchangeable ions show variations from soil to soil as great as those exhibited by the soluble cations. In some soils calcium is the predominant ion, in other potassium. It is of interest that in no case does sodum predominate, though in some instances its concentration is high. In general, the supply of all ions (soluble + exchangeable) is abundant from a nutritional point of view, and in one case only (soil 8) could ionic concentrations be regarded as exceptionally high.

Sulphate occurs in very small amounts. In only one soil could sulphate be detected qualitatively, the concentration in this case being of the order of 500 ppm.

Soil-plant relationships

A comparison of the constituents of the plant with those of the soil shows that there is no close correlation between the two. It is difficult to know which soil fractions should be used as a basis for the comparison. The available soil constituents probably are the soluble ions plus exchangeable, but on this basis no apparent relationship exists. Similarly, using the soluble ions only as the readily available soil solution no correla-

TABLE II. Some properties of soils supporting saltbushes in western New South Wales. Abbreviations: S = sandy; L = loam; C = clay; G = gravelly. Descriptions of the great soil groups unique to Australia are given by Prescott (1931) and Stephens (1953)

Soil No.	Locality	Great Soil Group	Texture Surface-Sub Surface	Structure	Colour	pH	Soluble Ions ppm.				Exchangeable Ions ppm.			Total P. ppm.	Organic Carbon %
							Ca	Na	K	Cl	Ca	Na	K		
1	Hay	Grey and brown soils of heavy texture	SL-SC	granular	lgt. brown	6.3	23	44	35	32	373	48	277	140	0.38
2	Hay	as 1	C-C	nutty	brown	6.3	166	561	15.2	1107	1800	932	347	200	0.62
3	Hay	as 1	SCL-SCL	nutty	lgt. brown	6.3	24	122	26	111	416	58	341	167	0.33
4	Bourke	as 1	C-C	nutty	dk. brown	8.0	52	64	3.7	42	4697	357	401	150	0.44
5	Bourke	as 1	C-C	nutty	dk. brown-grey	7.7	3.1	85	3.0	47	2559	425	523	95	0.37
6	Condobolin	as 1	C-C	nutty	dk. red-brown	7.5	20	290	6.3	222	1448	1176	643	125	0.48
7	Condobolin	as 1	C-C	nutty	dk. red-brown	7.5	50	397	5.1	550	1417	1248	487	142	0.37
8	Broken Hill (Salt Hole Creek)		CL-CL	cloddy	red-brown	7.5	505	3787	287	9250	234	875	1119	138	0.32
9	Broken Hill (Fowler's Gap)	skeletal	GCL-GCL	granular	red-brown	6.3	3.5	117	54	19	137	16	926	270	0.62
10	as 9	stony desert	CL-CL	nutty	red-brown	6.5	3.0	195	36	75	132	423	1079	225	0.42
11	as 9	stony desert	CL-CL	nutty	red-brown	7.5	2.0	97	41	43	239	89	941	245	0.41

tion exists, though from these figures some tentative hypotheses may be drawn up.

For individual ions, the most striking difference lies in the chloride. The percentage chloride is approximately the same in all plants irrespective of the concentrations of this ion in the soil; for example the plants growing on the soil with 19 ppm chloride actually contain more chloride in the leaf than those growing on soils with over 9000 ppm. It is interesting to note that the latter soil contains a much higher sulphate content than any of the others, and it is therefore possible that the sulphate ions may compete with the chloride.

The amount of calcium taken up bears no relationship to the external supply. The plants absorb very much less calcium than monovalent ions. Since magnesium occurs in lower concentration than calcium the tentative conclusion may be drawn that this element is absorbed according to the metabolic requirements of the plant and that a very small fraction of the total cations is represented by magnesium in the cell sap.

Sodium and potassium are of special interest. There is no close correlation between plant-content and soil-content of the two constituents. In Table III the ratios for plant and corresponding soil have been drawn up. When the Na/K ratio is at its highest, the uptake of potassium is not greatly suppressed. This may be taken to infer that the plant actually has a preference for K ions. In view of the fact that Na/K ratios for the soils are vague quantities in so far as the availability of the exchangeable ions cannot be stated quantitatively it is impossible to draw a definite conclusion from the data available. The results however, suggest further research on the following: the possible necessity for sodium and chloride in the nutrition of saltbushes; the possibility of replacement of potassium by sodium; the interaction of sodium and potassium. Experimental work to investigate these points is in progress.

TABLE III. Comparative data for sodium/potassium ratio calculated on ionic equivalents for the water soluble salts in the soil, and for the ash of the leaves of saltbush plants growing in the respective soils

Species	Soil No.	$\frac{Na}{K}$ Ratio (ionic equivalents)	
		Soil	Plant
A. vesicaria....	1	2.1	2.1
	2	60.2	3.6
	3	8.8	2.2
	4	30.0	2.9
	5	45.0	4.8
	6	58	3.8
	7	131	4.4
	9	3.6	6.1
	10	9.2	2.4
	11	3.9	2.0
A. nummularia..	8	22	1.9
	1	2.1	4.5
	6	58	2.9
A. inflata.....	3	8.8	8.5
	9	3.6	3.2

SUMMARY

Analytical data for some of the inorganic constituents of the leaves of three species of *Atriplex* are presented, together with analyses of the soils which support the plants.

The percentage ash for all plants is high (from 24% to 38% of the dry weight of the leaves). The ash consists chiefly of sodium and potassium, balanced by chloride. Calcium and magnesium

occur in small quantities relative to the monovalent ions. Phosphorus and nitrogen levels (ca. 0.15 and 3% respectively) are high in comparison with other native plants.

The soils supporting *Atriplex* vary tremendously in the mineral constituents mentioned above, but in spite of these variations the plants accumulate ions to approximately the same extent: For example, the extreme values recorded for chloride in the soils are 19 and 9250 ppm., whereas the extreme values for chloride in the leaves are 9.6 and 13.6% of the dry weight. Plants growing in these two extreme habitats appear the same as far as leaf form and size and general healthiness are concerned.

The ratio of sodium to potassium is of special interest. This ratio varies tremendously from soil to soil (extreme values: 2.1 to 131). In the plants, however, the ratio does not show such a wide variation (extreme values: 1.9 to 8.5) from which it may be inferred that the plants prefer potassium to sodium.

Further investigations under laboratory conditions on the importance of sodium, potassium and chlorine, and on the interaction of sodium and potassium, in the growth of *Atriplex* are being carried out.

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STUDIES IN HALOPHYTES III. SALINITY FACTORS IN THE GROWTH OF AUSTRALIAN SALTBUSHES[1]

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Introduction

Data relating to the salt accumulation by species of *Atriplex* growing in the field is presented in an accompanying paper by Beadle, Whalley and Gibson. The ecological significance of these salt accumulations is not known. It is in this point that the writers are primarily interested.

Other investigators have shown the responses to added salt are two:

(a) growth of certain species is increased with appropriate salt levels;

(b) growth of other species is limited to a greater or lesser extent by added salt.

[1] The authors wish to acknowledge the use of equipment and the cooperation of Mr. William V. Single, Dept. of Agr., N.S.W., Australia, in the freezing-point determinations, and the assistance of Miss Maisie Thode in the chemical analyses.

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Van Eijk (1939) analyzed the influence of NaCl and other salts on the growth of *Salicornia herbacea*. In the experiments *Salicornia* showed slight to greatly increased growth at the lower levels of all salts added. Adding additional Na_2SO_4 did not further stimulate growth. NaCl and KCl evoked greatest response at intermediate concentrations over the range 0.08 to 0.67 molar.

Fireman and Hayward (1952) carried out another type of study in which desert plants were shown to have widely differing chemical effects on the soils in which they were growing. Analyses of plant parts showed those plants which affect a soil property such as exchangeable sodium percentages also were those which accumulated large amounts of salt.

Further reference material available includes work by Bower and Wadleigh (1949), Eaton (1942), Richards, et al. (1954), and Wood (1925).

Aim of experiment

Two aspects of plant response to salinity were examined in these experiments. First, nutritional requirements for Na and Cl, and the possibility of Na substituting for Ca or K were tested. Second, the influence of added salts at increasingly high osmotic values was studied. Na as NaCl or Na_2SO_4 and Cl as NaCl or KCl were added in isonormal amounts.

Materials and Methods

Plants of *Atriplex inflata, Atriplex nummularia,* and *Lycopersicum esculentum* var. Grosse Lisse were used. Seeds of *A. inflata* free from the fruiting bracteoles were sown in vermiculite (expanded mica) and after an initial two waterings with a salt solution containing other nutrients, but not Ca, K, Na or Cl, watered with distilled water. The solution from a 1:1 aqueous mixture of the vermiculite contained 5 ppm Na, 11 ppm K and 1 ppm Ca. "Fruits" of *A. nummularia* were planted and treated as for *A. inflata.* Before planting, the "fruits" were leached 12 times with twice their volume of distilled water to remove Na, Cl and other ions from the bracteoles. The final leachate, 700 ml, contained 8 ppm Na, 16 ppm K and 5 ppm Ca. A test for Cl was not made. Seed of *L. esculentum* was planted in throughly washed sand. Upon reaching the cotyledon stage, the seedlings were placed in cotton-wool plugs and transferred to holes in masonite tops previously impregnated with paraffin wax over 4-liter enamelled pots of nutrient solution. All pots contained number one Hoagland's nutrient solution (Hoagland and Arnon 1950) except the minus calcium and minus potassium treatments, in which sodium was substituted for those ions respectively. The amounts of anions remained the same in the original solutions.

The seedlings were maintained in the above nutrient until good growth was established. Designated pots then received added salt as NaCl, Na_2SO_4 or KCl. The *Atriplex* containers were made up to 0.05, 0.2, 0.4, and 0.6 M of NaCl and KCl; 0.025, 0.1, 0.2, and 0.3 M Na_2SO_4. In terms of milliequivalents per liter these values for the cations respectively are 50, 200, 400 and 600 meq/l. All pots to receive salt were initially brought to 50 meq/l. One week later all except the 50 meq/l level pots were brought to 200 meq/l. After 2 more weeks the appropriate pots were brought to 400 meq/l, and after a further three weeks the last pots were brought to 600 meq/l. The plants of *A. inflata* were 4 weeks old from the cotyledon stage at the time the first salt was added; of *A. nummularia,* 5 weeks.

The tomato plants were treated in a similar manner. Differences were that they were relatively larger when the salt was added, and that only 50 and then 200 meq/l solutions were used. At the time of bringing to 500 meq/l the plants were 3 weeks old from the cotyledon stage.

All treatments were replicated four times. The pots were set out in a randomized-block design (Snedecor 1946). The blocks were arranged linearly on a glasshouse bench, two blocks on the north and two on the south side of the house. The *A. nummularia* pots had three plants, the *A. inflata* and *L. esculentum* two plants per pot. (Fig. 1.)

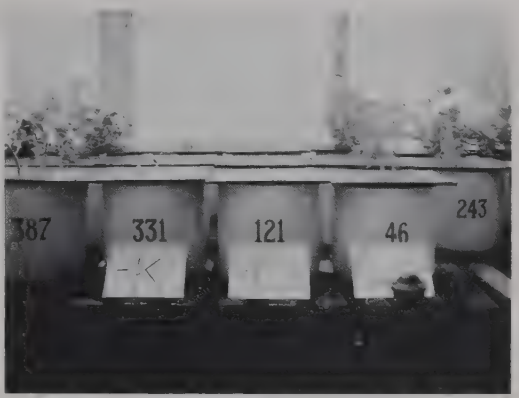

Fig. 1. Each row, front to rear, tomato, *Atriplex inflata* and *A. nummularia* plants. Left to right, solution cultures deficient in K, Ca, and then complete.

Routine treatment consisted of replenishing the solutions with distilled water whenever the level fell markedly. Occasional red spider build-ups on the control and low-salt plants necessitated spraying all plants with E-605 "Folidol" (parathion). As the plants grew the solution level was dropped from just below the pot rim to 2 cm. below the rim. This permitted roots with ample root hairs to develop.

In the last weeks before harvest, the water-use per pot was determined. The "full" water level was marked with red finger nail polish. The amount of distilled water necessary to bring each pot to level was then recorded at the time of replenishing the water.

The saltbushes were started in the solution cultures about the middle of winter, in August. At that time daily maximum temperatures in the unheated glasshouse were 70°F. or higher. Daily minimum temperatures did not go lower than 50°F. By harvest time toward the end of December, maximum temperatures were over 80°F., occasionally reaching over 90°F. The water-loss

determinations were made in this period of higher temperatures. Minimum temperatures then approximated 65°F. Relative humidities throughout the growing period generally reached nightly values of 90%. Minimum humidities of 60% were common, of 40% or lower of much less common occurrence. Relatively sunny weather was the rule.

The tomatoes, which were grown from the middle of September to the beginning of November, experienced springtime maximum temperatures rising from 70°F. to 80°F. and minimum temperatures rising from 55° to 60°F. during their growth period.

During the period between planting and harvesting, observations were taken on gross morphology, vigor, leaf discoloration, evidences of necrosis, vesicle appearance and other phenomena. Prior to harvest leaf thicknesses were determined to the one-thousandth of an inch with a spring-type micrometer. Following the cutting-off of the tops at harvest, notes were made on sap-exudation from the cut stumps. Leaf samples were taken from the *Atriplex* species on several occasions to obtain information regarding salt and water content. For *A. nummularia* the fifth pair of large expanded leaves back from the main growing tip for all three plants per pot was used. An average length shoot of the small-leaved *A. inflata* was taken, and the whole shoot or just the leaves were utilized at various times.

For one block each of the saltbush species the final "leaf" harvests were analyzed in several ways. Samples were first frozen, then thawed and the sap expressed in a plant press. The expressed sap was analyzed for Na, K, Ca, and Cl. Freezing point determinations were made on 1.6 ml. samples using the method described in Crafts, Currier, and Stocking (1949, pp. 93-95). Determinations of pH values were made with a B.D.H. Universal Indicator (British Drug House, pH range 4.0-11.0) on this same sap. One portion of the *Atriplex* leaf samples was ashed for mineral content analyses, another dried and boiled in distilled water for Cl analysis. The solutions in which these plants were growing were likewise analyzed for Ca, Na, K and Cl, as well as for pH values. The methods used for the chemical analyses are described by Beadle, et al. (1957).

At harvest fresh weights were taken of the tops. They were then oven dried at 60°C., and weighed when in equilibrium with room air. Dry weights of the roots were taken after air-dried for two weeks in the glasshouse. The period to harvest for *A. inflata* was 18 weeks, for *A. nummularia* 19 weeks, for tomato 7 weeks.

Results and Discussion

(A) Dry weight; top-root ratios; leaf dimensions

Table I gives the dry weights for the three species under all treatment conditions. Essentially no growth was made on the minus Ca and minus K solutions. In all but one instance (the minus K tomatoes), all plants of these treatments were dead before the experiment was terminated. The minus-Ca *Atriplex* plants died within two months after transferring to the solutions, the tomatoes within one month. Within each series of added salt solutions, greatest growth by *Atriplex* generally took place at the 50 meq/l level (approximately two atmospheres). This salt level somewhat depressed tomato growth, which was much depressed at the 200 meq/l. Both *Atriplex* species showed increased growth with certain levels of added salt, the greatest responses being to NaCl, then KCl, and lastly Na_2SO_4. *A. inflata* growth was not stimulated by the two higher levels of Na_2SO_4. Essentially all plants of both *Atriplex* species died shortly after being raised to the 0.4 and 0.6 M levels of KCl. Some *A. inflata* plants died under several of the other salt conditions, but not in a systematic manner which could be attributed to specific treatments. Additional *A. nummularia* plants were observed to die at the 0.2 M level of KCl and the 0. 6 M level of NaCl.

Table I. Mean total dry weight per plant

Culture Solution	Molarity	Cations meq/l	Species		
			Atriplex inflata 18 weeks (grams)	*Atriplex nummularia* 19 weeks (grams)	*Lycopersicum esculentum* 7 weeks (grams)
Complete			3.8± 1.8*	4.3± 1.2*	6.5± 0.9*
Complete plus NaCl	0.05	50	9.4	8.8	5.1
	0.2	200	9.3	9.3	2.0
	0.4	400	8.7	9.0	
	0.6	600	6.6	7.4	
Na_2SO_4	0.025	50	6.5	6.3	5.5
	0.1	200	6.2	6.6	2.1
	0.2	400	3.8	7.2	
	0.3	600	3.8	5.8	
KCl	0.05	50	8.9	7.6	5.3
	0.2	200	4.8	6.2	2.3
	0.4	400	1.4	2.5	
	0.6	600	1.2	2.0	
Complete minus Ca	...	...	0.0	0.0	0.0
K	...	...	0.0	0.0	0.0

*The fiducial limits of the arrays of means were computed in the analysis of variance for the complete and complete-plus-salt treatments. F tests at the 1% level showed that the effect of treatment was very significant for all three species.

The top-root ratios for the saltbush plants receiving added salt were higher than they were for

the control plants. Tomatoes showed a reversed response, with the top growth being relatively depressed.

Leaf length and leaf width of the saltbushes, which tended to parallel the dry weight results, were greater with lower levels of added NaCl and KCl. Increasing salt concentrations resulted in less lengthened leaves, or smaller ones at higher KCl levels. Leaf thickness of *A. nummularia* increased with added salt, especially NaCl, where the response was increasingly great with concentration, and KCl. *A. inflata* leaves were thicker than the controls only at the highest salt levels of NaCl and Na_2SO_4, the 0.2 M level of KCl. Likewise, percent leaf moisture was greater with the NaCl and KCl. Miller (1938) attributes a measure of drought resistance in tobacco to the increased leaf succulence brought about by the Cl ion.

(B) Observations on flowering; resistance to pests; appearance

Flowering, of the *A. inflata* only, took place under the control, 3 levels of NaCl, all Na_2SO_4, and one KCl level. Fruit was formed, up to the time of harvest, at the highest levels of successful growth for all three salts. Those fruits on the NaCl treatments were most advanced. All the seeds formed were viable.

Infestation of the plants by red spider or mite necessitated spraying with parathion. Only the control plants of *A. nummularia* were so infested (on one occasion). Several times the *A. inflata* plants required spraying. Despite their being randomly mixed in each of the four blocks, only those at the 50 meq/l cation levels and the control plants were infested. All plants received the spray.

In the last weeks before harvest gross observation of the plants on the benches showed a yellowing. This was not relieved by adding NH_4NO_3, nor did ferric sequestrene or ferric tartrate solutions applied to the leaves induce greening. The variation in size of plant suggested nutrient depletion would not be a uniform occurrence. Actually the plants with the greatest dry weight, those of *A. nummularia* at the 2 higher levels of NaCl, were green and very healthy in appearance.

Close examination of all the *Atriplex* plants showed a characteristic type of color change for each salt treatment. Very roughly, under presumably unfavorable KCl conditions, the whole plant turned yellow or ashen, many dying at the higher salt levels. Where damage was associated with Na_2SO_4 it usually was manifested as death of leaves. Na_2SO_4 plants, and the control plants of *A. nummularia*, manifested quite a bit of interveinal chlorosis. Symptoms of NaCl toxicity were chlorosis or necrosis of parts of individual leaves. The 200 meq/l salt levels led to death of all tomato leaves except young ones near the growing point.

Vesicles, as described by Black (1954), had a somewhat variable appearance depending on the salt level of the nutrient solutions. This variability in appearance of the leaf surface was best observed in *A. inflata*. Appressed plates were observed at the 0.4 and 0.6 M levels of NaCl and also on those plants which survived in the 0.2 and 0.4 M KCl. There was only a tendency to the formation of appressed plates at the 0.2 and 0.3 M levels of Na_2SO_4. Loose plates were formed at the 0.2 M level of NaCl and KCl, and somewhat so at the 0.1 level of Na_2SO_4. The control plants and all plants receiving only 50 meq/l of the several cations had fine scurfy scales.

(C) Ash analyses

The results of the analyses for ashed leaves are given in Table II. These figures show the following points.

The percentage ash for all plants exceeds 20%, which is abnormally high in comparison with glycophytes. The percentage ash and the concentration of the external solution are not arithmetically related. On the contrary, the plants build up a certain high concentration of ions, irrespective of the external concentration, and with the increase in the latter there is further increase in ash-content.

As far as individual ions are concerned, the uptake of K was appreciably higher than the uptake of Na at an equivalent external concentration. Also when K and Na are supplied together, as in the NaCl and Na_2SO_4 series (the K coming from the Hoagland's solution) K enters the plant more rapidly than Na (compare Na/K ratios of culture solution and ash).

The absorption of K from solutions of high concentration is so high that the plants are damaged, and are ultimately killed, as in case of 0.6 M KCl solution.

The uptake of Na was greater from NaCl than from Na_2SO_4 solutions which were at an equal normality for Na.

It is suspected that high concentrations of K precludes the entry of Na. Much of the Na which is recorded in the ash for the KCl series doubtless comes from dust from the leaves (the plants were grown in the City of Sydney) and from the glassware. The actual amount of Na recovered in the plants is much greater than that added as impurities in the salts. Furthermore, an amount approximately equal to the amount added as impurities was recovered from the solutions at the

TABLE II. Ash analyses of oven-dried leaves of two species of *Atriplex* grown in Hoagland's solution (complete), and with the addition of NaCl, Na_2SO_4, or KCl

Note: * indicates that the figure is inaccurate possibly because of contaminations.

Culture Solution	Cations meq/l	*A. nummularia*				*A. inflata*				Culture Solution
		Ash %	Na %	K %	Ratio $\frac{Na}{K}$ (ionic equivalents)	Ash %	Na %	K %	Ratio $\frac{Na}{K}$ (ionic equivalents)	Ratio $\frac{Na}{K}$ (ionic equivalents)
Complete.....	...	20.8	0.032*	8.03	0.005	26.1	0.056*	8.33	0.011	0.0072
Compl. + NaCl...	50	29.5	6.37	3.08	3.5	26.9	5.26	3.95	2.2	8
Compl. + NaCl...	200	35.4	8.65	3.26	4.5	31.4	7.70	2.33	5.9	33
Compl. + NaCl...	400	39.5	12.5	1.32	16.2	39.6	8.89	1.90	7.9	67
Compl. + NaCl...	600	46.0	13.6	1.09	21.2	54.0	16.3	1.15	24.5	100
Compl. + Na_2SO_4.	50	29.7	7.29	3.17	3.85	25.0	5.34	3.86	2.3	8
Compl. + Na_2SO_4.	200	32.1	8.56	1.76	8.3	27.3	6.33	2.10	5.1	33
Compl. + Na_2SO_4.	400	38.9	10.62	1.53	11.8	27.7	6.66	2.67	4.3	67
Compl. + Na_2SO_4.	600	33.4	8.8	1.45	10.3	52.1	13.6	1.87	12.3	100
Compl. + KCl....	50	35.6	0.085*	16.1	0.009	38.8	0.082*	13.9	0.012	0.002
Compl. + KCl....	200	52.5	0.163*	23.7	0.012	49.1	0.030*	23.7	0.002	0.002
Compl. + KCl....	400	58.0	0.100*	27.8	0.006	62.4	0.098*	29.0	0.006	0.002

end of the experiment (see below). The recovery of 2 to 5 times as much chlorine in the supposedly Cl-free plants as could be accounted for as impurities confirms this view.

(D) Analyses of expressed sap

Analyses of the expressed sap of the leaves of *A. nummularia* are given in Table III. The trends shown by these figures are in close agreement with those for the ash. Some additional data are available, namely Ca and anion levels.

It is of interest that the amount of Ca (which is always low relative to the concentration of the monovalent ions) increases with increasing Na concentration to a much greater extent than it increases with increasing K concentration. This point is unexplained.

As far as the anions are concerned, chloride and sulphate make up most of the balancing ions. Phosphate is relatively low. Nitrate, which has not been estimated quantitatively, occurs only in minute amounts, which are insignificant with regard to ionic balance.

In all cases there is a deficiency of anions as far as ionic balance is concerned. No attempt will be made to explain this disbalance at the moment.

There is a close correlation between cell sap concentration and osmotic pressure (see below).

(E) Analyses of culture solutions

Analyses of the culture solutions were done in the first place to ascertain the amount of certain ions added as impurities. Later, when unexpected high amounts of sodium and chlorine were recovered from the plants grown in solutions supposedly low in or free from these elements, an analysis of the culture solutions were made to see how much, if any, of these elements had been left by the plants. Extreme caution against contamination was taken when these solutions were being analysed.

The results are given in Table IV. They bring out some most interesting points. Firstly the solutions have been depleted of the chloride ion. Secondly in those cases where the Na concentration was originally very low (which means that the ratio of K to Na was very high), the sodium ions have not been removed or even reduced in amount. It is this set of figures that throws suspicion on the Na analyses of the ashed leaves. Thirdly the presence of K in the complete solution suggests that the plants were at no time short of this element.

(F) pH values

The sap expressed from saltbush leaves, either fresh or first frozen in dry ice, gave pH values of 5.5-6. *A. nummularia* leaves collected a few weeks later, at harvest, and first frozen to −16°C. in a deepfreeze, gave somewhat higher values, from pH 6 for the control plants to pH 6-7.5 for the plants with added salts.

Fresh culture solutions were at pH 5. Those solutions where little growth took place because of Ca or K deficiency or salt toxicity showed little or no change in pH by the termination of the experiment. Changes in pH values were sometimes marked, and rather variable, for those solutions showing good plant growth. The *L. esculentum* solutions tended to become alkaline, reaching pH 7.5 or higher in instances for all treatments. Only at the 0.05 N level of the plus-salt solutions did the *A. inflata* solutions go as high as

TABLE III. Analysis of expressed sap of a series of *Atriplex nummularia* plants grown in Hoagland's solution (complete) with the addition of NaCl, Na_2SO_4, or KCl

Note: (1) The sulphate analyses are semiquantitative only.
(2) * indicates that the figures are very low, possibly inaccurate because of contaminations; more accurate data are given in Table 2.
(3) + indicates that the figure is under suspicion.

Culture Solution	Cations meq/l	Ion Concentration mg/cc Sap						Cations	Anions
		Ca++	Na+	K+	Cl^-	SO_4=	HPO_4= as P	Ca++ + Na+ + K+ m.e./cc. sap	Cl^- + SO_4= + HPO_4= m.e./cc. sap
Complete	...	0.085	*	6.90	0	1.48	0.37	0.198	0.054
Compl. + NaCl	50	0.215	8.00	3.50	11.14	1.92	0.104	0.447	0.368
Compl. + NaCl	200	0.195	9.87	2.60	12.00	1.92	0.164	0.499	0.388
Compl. + NaCl	400	0.380	16.75	1.60	23.20	0.96	0.070	0.787	0.674
Compl. + NaCl	600	0.405	20.00	1.80	29.6	1.92	0.180	0.934	0.872
Compl. + Na_2SO_4	50	0.170	7.00	2.90	0.142+	3.36	0.330	0.387	0.094
Compl. + Na_2SO_4	200	0.265	12.12	1.25	0.142+	13.9	0.127	0.576	0.302
Compl. + Na_2SO_4	400	0.270	12.25	1.75	0	13.9	0.202	0.598	0.303
Compl. + Na_2SO_4	600	0.330	14.75	2.35	0.142+	21.2	0.356	0.613	0.466
Compl. + KCl	50	0.073	*	16.75	10.72	0.72	0.126	0.420	0.326
Compl. + KCl	200	0.088	*	25.90	19.50	0.72	0.137	0.748	0.574
Compl. + KCl	400	0.100	*	31.75	24.00	1.58	0.287	0.831	0.727

pH 7.5. The *A. nummularia* values reached pH 7.5 at all NaCl levels, the lower levels of KCl, and the control solutions.

(G) Osmotic pressure and percent moisture

From Table V we find that the osmotic pressure of expressed *Atriplex* juices is very appreciably greater than that of the solutions in which the plants grow. The values for the two species agree well except for such instances as those in which the *A. inflata* sap was diluted to achieve freezing within the range of the salt-ice bath on the day of the determinations. In such cases, at the 0.6 M level of NaCl and the 0.1 M level of Na_2SO_4, the O.P. calculated for *A. inflata* was nearly double that recorded for *A. nummularia*. At harvest, solution O.Ps. of the two species were very similar. Values for NaCl and KCl were in the same order as the normalities of added salts (2:8:16:24). For Na_2SO_4 the values were in the order 2:5:10:14. Control solution values on this basis would be approximately one-half atmosphere. The O.Ps. for the expressed sap from control plants, however, were not greatly lower than those for plants at the 0.05 N level of the various cations. The ratio of plant O.P. to solution O.P. therefore narrows from roughly 30:1 with the control plants to 2:1 for plants at the highest salt levels. The plus-salt plants, maintained an O.P. about 16 atmospheres greater than the solutions on which they were grown.

TABLE IV. Analyses of solutions before and at the end of the experiment for Na and Cl added as impurities to solutions supposedly lacking these elements. Where the S.D. is given, the figures are based on three estimates; where no S.D. is given the figures are means of two duplicates

Culture Solutions	Cations meq/l	Concentration of Ions (ppm)					
		K		Na		Cl	
		Original	Final	Original	Final	Original	Final
Complete (supposedly lacking Na and Cl). A. numm.	...	....	1.4	1.0	0.9±0.3	1.5	0
Complete (supposedly lacking Na and Cl). A. infl.	...	....	5.0	1.0	1.2±0.1	1.5	0
Complete + Na_2SO_4 (supposedly lacking Cl)	50	....	....	....	....	2.5	0
	200	....	....	....	....	5.3	0
	400	....	....	....	....	9.1	0
	600	....	....	....	....	13.0	0
Complete + KCl (supposedly lacking Na).	50	....	....	2.8	1.6±0.8		
	200	....	....	11.2	12.1±2.8		
	400	....	....	23.0	21.6±5.4		
	600	....	....	34.3	31.7±8.6		

TABLE V. Osmotic pressures determined at harvest by the freezing-point method

Culture Solution	Cations meq/l	Expressed Sap		Nutrient Solution	
		Atriplex nummularia (atmospheres)	Atriplex inflata (atmospheres)	Atriplex nummularia (atmospheres)	Atriplex inflata (atmospheres)
Complete		16.0	13.1	0.3	0.6
Complete plus NaCl	50	17.6	17.4	1.7	2.1
	200	24.0	25.8	7.9	7.5
	400	31.6	39.4	14.7	15.7
	600	41.5	74.4*	23.3	23.9
Complete plus Na_2SO_4	50	16.5	17.0	1.8	2.1
	200	20.0	37.0*	4.9	5.3
	400	22.6	28.5	9.5	9.8
	600	27.0	32.4*	13.3	13.8
Complete plus KCl	50	18.6	19.8	1.7	2.5
	200	26.1	32.2	7.7	7.6
	400	30.1	....	15.8	17.2
	600	54.8	....	23.9	23.7

*Sample diluted 1:1 with distilled water to achieve freezing.

The O.P. values for the expressed sap of *A. nummularia* are plotted against the chemically determined total cations of the sap in Figure 2.

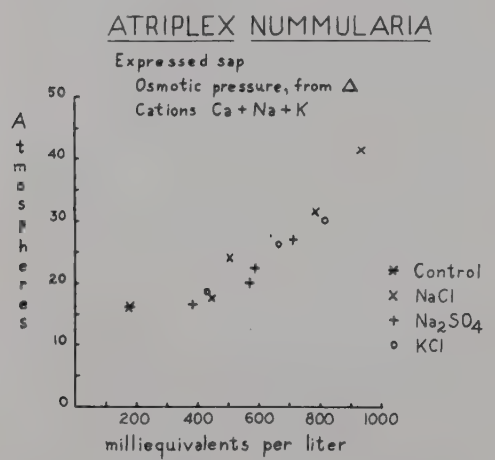

FIG. 2. Osmotic pressure related to cation content of expressed sap.

Here again the O.P. of the plants on the control solution is much higher than its salt content would indicate in comparison with plants receiving added salts.

The percentage moisture, dry-weight basis, for the *Atriplex* plants on the control nutrient solutions was approximately 350%, in contrast to more than 1000% moisture on a dry-weight basis for tomato. Leaves alone of *Atriplex* were closer to 500%. All species showed an increased moisture content with the lower salt concentrations employed. For the two *Atriplex* species, percentage moisture was greatest with KCl, next with NaCl, and least with Na_2SO_4 (actually *A. inflata* had a lower moisture content for all levels of Na_2SO_4). Only *A. nummularia* showed an increased percentage moisture at the higher salt concentrations employed, and then only with NaCl.

The increased percentage leaf moisture with added salt can well be explained as a simple salt hypertrophy resulting from the increased osmotic pressure. However, straight line relationships between leaf size or thickness, osmotic pressure and salt concentration do not exist, possibly because of four factors, namely, (a) differences in dissociation of the salts at different concentrations and (b) there is a limit to which cell walls can be stretched. (c) In the calculation of percentage moisture the dry material of the leaf consists not only of organic materials, but also of inorganic salts. (d) Osmotic pressures do not always represent the O.P. of the cell sap itself since in some cases epidermal vesicles had broken and salt crystals had formed; this dry salt is dissolved in the cell sap as it is pressed out. It is worth mentioning here that high osmotic pressures for *Atriplex* quoted by some writers are possibly due to the same effect.

(H) Water use

Table VI shows the water use over a two week period per gram dry weight of tops, live plants only. If we consider first the tomato results (here a five-day period), at 0.05 N water loss was not significantly influenced, though it increased with NaCl and Na_2SO_4 and decreased somewhat with KCl.

Additions of salt to the *Atriplex* species resulted in less water use with the Na salts. Actually water loss per gram dry weight was significantly less in the *A. nummularia* series with all amounts of added NaCl and Na_2SO_4. The healthiest looking and largest *A. nummularia* plants were those receiving NaCl. In fact, the plus-salt *Atriplex* plants which used proportionately less water than the controls all had increased dry weights, except the *A. inflata* at 0.2 and 0.3 M Na_2SO_4. Eaton (1942) found a lower water requirement with his lower levels of added salt only. He related the enhanced water requirement at higher salt levels to the smaller relative size of plants and the resulting greater insolation and wind movement under field conditions.

Following decapitation at harvest, only the tomato stumps showed sap-exudation. Plants on

TABLE VI. Daily water use per gram dry weight of top at harvest

Culture solution	Cations meq/l	Species: Atriplex inflata (Milliliters)	Species: Atriplex nummularia (Milliliters)	Species: Lycopersicum esculentum (Milliliters)
Complete	...	9.4± 2.0*	9.5± 1.5*	19.8± 5.1*
Complete plus				
NaCl	50	6.2	4.7	20.8
	200	5.1	3.6	
	400	3.2	3.4	
	600	...	2.7	
Na_2SO_4	50	5.9	6.0	25.0
	200	4.4	5.1	
	400	5.4	3.9	
	600	...	4.1	
KCl	50	7.9	7.1	17.0

*The fiducial limits of the arrays of means were computed in the analysis of variance. F tests at the 1% level established that the effect of treatment was very significant for *Atriplex inflata* and *A. nummularia*. Significant differences were not found for *Lycopersicum esculentum*.

the complete solutions exuded copiously, which slowed down and stopped after 4 days. Tomatoes at the 50 meq/l level of all three cations exuded to a lesser extent, for two days, while those at the 400 meq/l levels did not show sap exudation.

DISCUSSION AND CONCLUSIONS

There is no doubt that these two species of *Atriplex* have the usual requirements for Ca and K and that Na cannot be substituted for either of these elements. Saltbushes, however, differ from other plants, such as tomato, in that they grow so much better with added salt. From the data available the optimum cation-concentration appears to be 50 meq/l, or possibly less. The kind of ions supplied to the plant appears to have some significance which cannot yet be fixed. However, the dry weight figures (Table I) suggest that chloride is preferable to sulphate as an anion and that a mixture of Na and K (complete + added NaCl) is more effective than a solution very high in K.

The data bring out some interesting points on the function of Na. This element is apparently not essential as a nutrient. When supplied to the plant in large amounts it is absorbed in quantities which are dependent on the ratio of Na/K in the external solution. It appears that K enters the plant more rapidly than Na so that when the Na/K ratio in the external solution is low (0.002) probably only K enters the plant. Further to this, when the concentration of K is high, 600 (and 400) meq/l, and the Na/K ratio at the 0.002 level, K enters in such large quantities that the plants are killed. The toxic levels for K in the external solution may be much lower if experiments were continued longer, when the internal concentration of K could become much higher. Under these conditions Na therefore must be regarded as essential for the normal growth of these plants, its function being protective against lethal concentrations of K which result from the more rapid uptake of K ions. It is clear that both the ratio and the concentrations are important and further work to determine the optimum and critical values is needed.

In this connection we may review other findings on the role of sodium in plants known to accumulate it. Miller (1938) stated as an alternative hypothesis that Na seems to retard the absorption of K. Also, van Eijk (1939) showed *Salicornia* to grow much better with a KCl-NaCl mixture than with higher levels of KCl alone. Kaudy, *et al.* (1953) found on a series of Wisconsin soils where the Na/K was 1:10 that upper leaf tissue of sugar beets had a ratio of 1:2, again showing a greater rate of uptake of potassium. Their sampling disclosed a ratio of 1:17 at the base of the root, 1:8 in young leaf blades, and 1:1 in aged blade tissue. Lehr (1947) described sodium to be essential for the proper development of the beet plant on humic sandy soils in Holland. The role of sodium was related to the potassium, and the calcium, status of the soils. Eaton (1942) reported little if any evidence of interactions between sodium and potassium accumulation. In his work chlorides or sulfates were added, as mixtures of sodium, calcium, and magnesium salts.

In the present study added salts in the external solution lead to enhanced salt content and increased osmotic pressure of expressed sap, and decreased water loss from the saltbush leaves. These results are in agreement with data for halophytes generally, such as those given by Adriani (1956). The increased osmotic pressure can be rather directly related to the greater salt content of the sap, and both these factors lessen evaporation from solutions. Thus evaporation from sea water is 5% less than it is from fresh water (Internt'l Critical Tables, 1929). The expressed sap from the plants grown in 200 meq/l solutions is approximately the same osmotic pressure as sea water, while that from the 600 meq/l chloride plants is roughly double that of sea water. Under field conditions, since the surface dead vesicles are mixed with salt crystals the salt solution at the evaporating surface must be near to saturated, and under these conditions the salt solution must have a considerable protective function.

A further point of ecological significance sug-

gested by this experiment relates to the rate of growth and of flowering and the advantages of these in the occupancy of an area. The presence of salts in the soil leading as it does to added growth must be of significance with regard to competition with plants of other species, and possibly of greater significance still is the hastening of flowering and fruit formation when salt is present; this must be of considerable advantage to plants growing in areas where the water supply is restricted.

Lastly the susceptibility of control plants (also plants of *A. inflata* at 50 meq/l levels) to pests such as red spider, in contrast to plants taking up higher levels of salt, shows that added salt may be an important factor in protecting plants from such infestation. The occurrence of animal pathogenic damage may tip the scale for a species to an unfavorable competitive relationship with regard to accompanying species in an area.

Summary

1. Two Australian saltbush species, *Atriplex inflata* and *A. nummularia,* as well as *Lycopersicum esculentum* var. Grosse Lisse, were grown in nutrient-solution culture.

2. The series of nutrient solutions used included Hoagland's alone or with additions of NaCl, or KCl, at 0.05, 0.2, 0.4, and 0.6 M levels for the saltbush species. Na_2SO_4 was added at 0.025, 0.1, 0.2, and 0.3 M levels. These solutions resulted in 50, 200, 400 and 600 meq/l values for the respective cations. Solutions at 50 and 200 meq/l only were used for the tomatoes.

3. The saltbushes produced much greater dry weight with added salt, somewhat irrespective of the salt added.

4. Osmotic pressures of the saltbush leaves, which were related to their salt contents, tended to show a more or less constant absolute value greater than the solutions. This resulted roughly in a range from 30 times that of the nutrient solutions for the control plants to 2 times that of the solutions for the plants growing in 600 meq/l solutions.

5. Daily water use per unit dry weight in the two weeks prior to harvest was much less for the saltbushes receiving added Na salts.

6. The tomatoes grew less to much less with added salt.

7. Both saltbushes and tomato essentially did not grow when Na was substituted for either the Ca or the K of the otherwise complete nutrient solutions.

8. Plants grown in solutions high in K, and very low in Na, died.

9. The presence of Na appeared to protect the plant against lethal concentrations of K.

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NOTES AND COMMENT

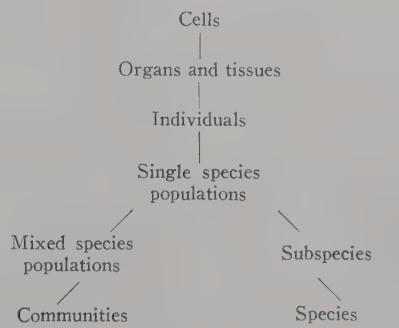
OBSERVATIONS ON THE STATUS OF ECOLOGY

The status of ecology with respect to its related fields and the biological sciences generally has been deplored by a number of ecologists for its lack of maturity and definition (Birch 1955; McMillan 1954, 1956; Park 1945). The essential objectives of ecology as a field of study and as a definitive science are rather poorly defined and, due to its broad interests and to the popularity of its concepts in related fields, it is often difficult to separate purely ecological research, directed toward the solution of fundamental problems in ecology, from that which has "ecological aspects." While we may correctly refer to ecology as "the study of the relations between an organism and its environment," this definition is too broad to clarify the scope of ecological research and it does not define the position of ecology with respect to the other biological sciences. Since an organism does not, and cannot, function outside an environmental context of some sort, we might easily infer from the above definition that all biological research is ecology. To some authors this seems to be the case, but unless ecology has certain characteristics which can be described objectively and which distinguish it from its related fields, there is no justification for maintaining that it is anything more than a useful but rather vague point of view.

While it is perhaps true in a sense that the essence of ecology does lie in its point of view, as Woodbury (1954) asserts, and that ecology is applicable in this form to a wide variety of biological problems, a statement of this sort merely signifies an awareness of the fact that plants and animals have environmental relations which govern the expression of their various attributes. As such, an ecological point of view may be a valuable research tool or method of interpretation, but it is not a qualified statement of the aims, the methods, or the scope of ecology. We expect for example that every modern biologist accepts the facts of evolution and that he uses an evolutionary interpretation whenever it is appropriate, but we usually reserve the term "evolutionist" for a comparatively small group of scientists who devote their research and thinking to the major problems of evolution, and who have made fundamental contribtuions to evolutionary theory. In other words, the mere acceptance of the fact of ecological relations or the use of an "ecological approach" need not imply research on the fundamental problems of the science of ecology, nor does it justify the label "ecologist," and in order to describe ecology as a definitive science we must, in some way, be able to describe a set of aims and concepts which are unique.

Dice (1955) contends that ecology has no natural boundaries and that any attempt to draw boundaries between ecology and its related fields would "do more harm than good." This assumption depends upon whether such boundaries are used to define the areas of research which ecologists are particularly concerned with or whether, instead, they place restrictions on the interpretation of ecological events and concepts. These alternatives are not inseparable and the latter is obviously as undesirable in ecology as it is in any field. But in spite of the above contention, Dice (1955) attempts to define ecology by its methods, its vocabulary, and the following list of concepts: levels of organization, energy relations, ecosystems, ecologic balance, reproduction, competition, variability, ecologic patterns, individual adaptability, evolution, and social cooperation. While he does not claim that "these or other concepts are exclusively the property of ecology as opposed to other sciences," certain of them, because they are not unique, cannot be regarded as definitive. Certainly concepts of reproduction, individaul adaptability, and evolution are just as appropriate, if not more so, to fields other than ecology. Dice is undoubtedly correct when he implies that concepts cannot be regarded as "exclusively the property" of any particular field, and this is perhaps even more true of experimental methods and techniques; but we may on the other hand indicate those concepts or methods which are especially applicable to research in a particular field, or which are primarily its concern. For example, McMillan (1956) argues that "Techniques such as the quadrat (cited by Dice, 1955, as definitive of ecology) and the bisect, which are used for dealing with spatial arrangements are geographical, not ecological tools." Obviously it is rather pointless to insist that spatial arrangements are the exclusive concern of geographers, since spatial arrangements are considered in virtually every field of science, even though they may involve different subjects or different levels of organization. In other words, it is not so much the quadrat method which is unique in this case, but rather the particular problems to which it is applied.

While ecologists use methods and concepts which are often common to its related fields, their interests tend to center on special levels of biological organization; namely, the biological properties of populations and natural communities. This fact is expressed in the following observation by Park (1955): "The distinguishing characteristic of ecology is its ultimate preoccupation, not with the individual organism, but with the environmental relations of groups. Thus the group, or population, emerges as a natural entity." In another paper Park states, "The subject matter of ecology can be considered under four categories, each of which represents a grade of biological organization of increasing functional and structural complexity. These four are: the individual organism, the single species population, the mixed or several species population and the community" (Park 1948). These categories are included in the following diagram of the different units or levels of biological organization:



In this diagram, subspecies and species, which we may regard as "taxonomic populations," are considered distinct from the "biological population" of the ecologist. While this is to some extent an artificial separation, the

systematist is usually concerned with statistical measures of variation in geographical units, whereas the ecologist deals with the biological properties, such as age structure, population growth, and population density, of local units which can usually be censused.

At each of these levels of complexity there are fields of study devoted to the structural or functional properties associated with that particular grade of organization. A series of examples is offered in the following tabulation of some of the principal subdivisions of biology and the levels of organization with which they are primarily concerned:

LEVEL OF ORGANIZATION	STRUCTURE	FUNCTION
Cells	Cytology	Cytology
Organs and tissues	Histology	Physiology
Individuals	Anatomy	Physiology
Single-species populations	Ecology Systematics	Ecology Genetics
Mixed-species populations	Ecology	Ecology Parasitology
Communities	Ecology Geography	Ecology
Subspecies	Systematics	Genetics
Species	Systematics Geography	Genetics

One must recognize, of course, that related fields are bound to have overlapping interests and that their research will often be directed toward similar, if not identical, problems; but this does not preclude their being separable on the basis of their primary concerns. It has often been pointed out that ecology uses methods borrowed from physiology (c.f. McMillan 1954), and some authors have in fact described ecology as "field physiology"; but the ecologist begins with the individual as his smallest unit of study and is primarily interested in the biological properties of populations and communities, whereas the physiologist is concerned more with individuals than with populations, even though he may study the effects of environment in certain situations. Ecology and genetics, on the other hand, are both concerned with the same level of biological organization in many cases, as with population genetics and population ecology; but the geneticist is only secondarily interested in the unit responses of populations to environmental factors, except in so far as the hereditary mechanism is involved (Odum 1953).

The above scheme gives little prominence to the traditional division between autecology and synecology, since it is felt that ecology is invariably concerned with group phenomena and ecological research is seldom, if ever, restricted to an autecological subject. The central theme of ecology is a list of concepts pertaining to group phenomena, most of which may be approached through the study of single-species populations, mixed-species populations, or communities. Furthermore, these concepts, such as food chains, the pyramid of numbers, competition, predator-prey relations, parasite-host relations, population growth, energy relations, and the natural regulation of numbers, each have structural and functional characteristics which tend to comprise one of the natural divisions of ecological study, and each lends itself to both descriptive and experimental study. Ecology has been rather strongly criticized for its emphasis on descriptive study (McMillan 1954), but surely its ultimate aim is a synthesis that will describe "not only the parts of a complex system but the interaction and balance between them, and the dynamic properties of the system as a whole" (Elton and Miller 1955). Community ecology has been particularly slow to progress from the study of structure to that of function and to enter an experimental phase of research, but the subject matter of community ecology is extremely complex and a vast amount of information from single- and mixed-species population relations is necessary before adequate synthesis at the community level is possible. If, however, our central aims are research on group phenomena such as those listed above, we may expect that the field of ecology will progress from description to experiment as measurements are substituted for generalized observations (Allen 1955), and that it will retain its specific identity through its concern with population and community relations. It is only within these areas of research that ecology can find a basis for a definitive status in the biological sciences.

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INTRA- AND INTERSPECIFIC CONFLICT OF MUS AND PEROMYSCUS[1]

The occasions in which house mice (*Mus musculus*) and native American mice, particularly *Peromyscus,* come into contact are numerous. Not only do the two genera meet in man-made buildings located near the native habitat of *Peromyscus,* but also in the field where *Mus* are occasionally found associated with *Peromyscus* far from human habitation. Despite the frequent association of these two genera, little is known about their interactions. Do they compete for food or shelter? Is *Mus* able to replace *Peromyscus?* If so, is this accomplished by overt aggression, by greater reproductive potential, or by better utilization of the available resources? The history of introduced animals is filled with their success in replacing native species by one or all of these methods. For example, the introduced gray squirrel (*Sciurus carolinensis*) appears to be successfully replacing the common squirrel (*S. vulgaris*) throughout many regions in England (Shorten 1953). On the other hand, intraspecific conflicts are often intense while individuals of another species may live in the same environment without conflict.

The purpose of the present experiment is to examine the aggressive behavior of *Peromyscus* and *Mus,* both in relation to other members of the same species and in relation to each other.

Methods

The animals in this experiment were sixteen male *Peromyscus maniculatus bairdii* and sixteen male *Mus musculus,* of the C57BL/10 inbred strain. The *Peromyscus* were descendants of a stock received from Dr. W. Prychodko, who obtained them from the Laboratory of Vertebrate Biology, University of Michigan. This stock of *Peromyscus* had been bred in the laboratory for seven years prior to the experiment. The *Mus* are an inbred strain maintained at the R. B. Jackson Memorial Laboratory (Snell 1952). Although the C57BL/10 strain has been derived from domestic mice, they are similar to wild *Mus musculus* (Calhoun 1956), and may successfully live as feral commensals, even breeding with wild *Mus.* They are known to be aggressive (Bauer 1956) but perhaps not more so than wild *Mus musculus* (Southwick 1955). Usually domesticated forms are less aggressive than their wild progenitors (Richter 1954).

Individuals of both genera were weaned at 30 days of age and caged individually until they were tested when mature at 6 to 10 months of age.

The tests were given in wooden boxes 6 x 6 x 12 inches similar to the cages used for housing the mice. A removable partition separated the combatants until the test began. One measure of aggressiveness was the number of encounters which resulted in a fight. Another measure of aggression was the fighting response latency (Fredericson 1949) which was taken as the elapsed time from the moment when the partition was removed until the first vigorous fight began. The frequency of running away, squeaking, nosing, grooming, and attacking preceding a fight was also recorded.

Procedure 1 consisted of giving eight mice of each species a series of five daily trials with seven other individuals of the same species in a round-robin fashion. Each trial lasted for a period of five minutes or until the mice began to fight, when the mice were separated in order to prevent dominance. This procedure tested for intraspecific aggression.

Procedure 2 consisted of taking the mice used in *Procedure 1* after mouse had fought every other individual of the same species and placing it with a mouse of the other species for two trials. Each mouse had two encounters with four individuals of the other species. The trials were five minutes in duration like those of *Procedure 1.* On the day following the individual tests, all the mice were placed in a large observation box 30 x 30 x 39 inches with wood shavings on the floor, activity wheel, food rack, water bottle, elevated nest box and ramp leading to the nest box. This procedure tested for interspecific aggression.

Procedure 3 employed eight different mice of each species in a series of five daily trials with individuals of the other species. Each trial lasted five minutes or until the mice began to fight. This procedure was essentially like *Procedure 2* except that the mice used in this procedure had not previously encountered any other mice, either of the same species or a different species.

Results

Intraspecific aggression. Since each animal had an opportunity to fight five times with the seven other individuals of its genus, there were 35 opportunities to fight in all. Of these 35 opportunities, the *Peromyscus* fought an average of 11.2 times, while the *Mus* fought an average of 34 times. There was no overlap in these frequencies. The individual *Peromyscus* which fought most frequently had 17 fights, while the least frequent fighter among the *Mus* fought 31 times.

The fighting response latencies of *Peromyscus* were significantly slower when tested by the Chi-square technique; significance was calculated from the number of pairs that fought before or after the two minute median ($x^2 = 10.28$; $P < .01$). The mean of fighting response latencies for *Peromyscus* was 4.01 min. while the mean for *Mus* was 0.84 min. The mean response latency of only those pairs of *Peromyscus* which fought is still considerably slower (3.63 min) than that of the *Mus.* This indicates that *Peromyscus* are less ready to engage in combat than the *Mus.*

The most significant difference in the prefight behavior of the two genera was in the frequency of nosing and grooming each other. *Peromyscus* engaged in both activities more frequently (noses: $t = 3.56$; $P < .01$; grooms: $t = 3.67$; $P < .01$) than *Mus.* Although the frequency of prefight behavior depends largely on the amount of time the mice have before fighting (response latency), these behavioral activities perhaps distinguish the aggressive characteristics better than any other measure. The frequent nosing and grooming behavior elicited by *Peromyscus* often suggested dominance without a fight. When the male *Peromyscus* approached and nosed each other, one usually began to groom the other. Any attempt of one individual to reciprocate the grooming led to vigorous grooming, from which either a fight developed or one member submitted to being groomed. The passive mouse then usually curled in a corner or sometimes rolled over on its back and allowed the active groomer free access to any part of its body. When the active mouse stopped grooming, it explored the cage and returned at intervals to resume grooming. The passive mouse rarely left the corner where he had been groomed. These differences in activity and grooming

[1] This study was supported by Grant MH-123 of the National Institute of Mental Health, U. S. Public Health Service.

strongly suggest that dominance may be established without overt fighting in *Peromyscus* in contrast to *Mus*, which rarely establish dominance without fighting vigorously.

Interspecific aggression. After the intraspecific patterns of aggression had been established by the round-robin pairings, the same individuals were paired with four members of the other genus for two trials. *Mus* attacked *Peromyscus* on the average of 20 times per trial or 40 times for each pair. None of the *Peromyscus* attacked *Mus*. The intraspecific patterns of behavior for each genus were maintained in the interspecific fighting situation. On the first encounter the *Peromyscus* usually started to groom the *Mus*, while the *Mus* soon began to attack the *Peromyscus*. In only one encounter of one pair did the *Peromyscus* attempt to fight back. All other pairings were typified by the frequent attacks of *Mus* upon *Peromyscus*. The latter assumed a defense posture, attempted to hide, ran away, or leaped wildly about the cage.

After the last test the *Peromyscus-Mus* pairs were left together for two hours. One *Peromyscus* was killed and two others were badly bitten by the *Mus* in this time.

Since the interspecific patterns of aggression established by the mice could have resulted from the previous intraspecific experience, eight additional mice of each species were brought together in pairs for five successive 5-minute trials (*Procedure 3*). These mice had been isolated since they were weaned at 30 days of age and had experienced no previous aggression.

The lack of previous aggressive experience appeared to inhibit the aggressive responses of both species during the first two or three trials. During these first trials most *Peromyscus* leaped wildly about the cage while the *Mus* carefully explored the cage. Only one pair had more than three contacts during the first two trials. Occasionally the *Peromyscus* jumped upon *Mus* as the former leaped about wildly. This type of treatment tended to intimidate the *Mus* and they sqeaked and ran way. By the fourth and fifth trials, however, the *Mus* began to attack the *Peromyscus*. The mean number of attacks by *Mus* was 16.0 per mouse, while *Peromyscus* attacked *Mus* a mean of 2.5 per mouse. Most of the *Peromyscus* attacks were accomplished by one mouse. A Mann-Whitney *U* test indicates that *Mus* attacked *Peromyscus* significantly ($P < .02$) more times than *Peromyscus* attacked *Mus*.

When all the mice of both species were placed together in the large observation box the *Mus* immediately began to attack each other and the *Peromyscus*. Since the *Peromyscus* quickly escaped from the *Mus* in the large box, only other *Mus* resisted the attacks of each other. The *Mus* did not discriminate in their fights with other individuals. After the first four minutes, the intensive fighting subsided and the *Mus* assumed a defense posture on approach of another *Mus*. Sporadic outbreaks of fighting still occurred at intervals as the aggressive individuals continued to attack and stir the entire group into fighting. Other than the sporadic fighting, the defensive attitude persisted in the *Mus-Peromyscus* relationships. When a *Mus* approached a *Peromyscus* the latter assumed the defense posture and no fight followed. During the fighting among the *Mus*, the *Peromyscus* tended to huddle together in a corner and to keep out of the way. At the end of the 45-minute observation period, most *Peromyscus* were huddled together in a corner; most *Mus* were grooming and licking their wounds, while two *Mus* kept making rounds attacking the defensive *Mus* from time to time.

The mice were kept together for three days. During that time the two genera made some adjustment to each other and they were occasionally observed huddled together. Fighting was not observed, although there were occasional disputes with a mild attack, chase, defense posture and squeaks among both genera.

The *Mus* were removed on the third day and only the *Peromyscus* were left. One of them became aggressive by the fourth day and actively chased the others. None of the other *Peromyscus* approached him.

Discussion

The greater aggressiveness displayed by *Mus* than *Peromyscus* under laboratory conditions suggests that whenever the two genera come into contact under natural conditions the *Peromyscus* may be attacked by the *Mus* and driven from the immediate region. However, it may well be that the two genera will occur in the same area under favorable conditions because *Peromyscus* does not resist the attacks of *Mus* and can easily escape the latter. Under unfavorable conditions, such as a high population density or a severe shortage of food or shelter, it is likely that *Peromyscus* are replaced by *Mus*. The type of interspecific competition need not result from the better utilization of environmental resources by *Mus* nor from their higher reproductive potential. Instead, the competition may take the form of overt attacks by *Mus* on *Peromyscus* as both genera are forced into more frequent contacts during population peaks.

The testing procedure demonstrated how the patterns of intraspecific aggression affected interspecific relationships. Different patterns of aggression were not displayed intraspecifically and interspecifically. Rather, the behavior a mouse showed toward its species-member was duplicated in its behavior toward a different species. *Peromyscus* tended to groom and huddle together, while *Mus* fought with each other. Consequently, when placed together, the aggressiveness of *Mus* was maintained and the initial attempts of *Peromyscus* to groom were replaced by escape behavior. When both genera were placed together in the large cage, the behavior patterns of each genus increased the frequency of intraspecific contacts. The *Mus* fought among themselves and the *Peromyscus* huddled together. This maintenance of specific patterns of behavior illustrates that the behavior of each species tends to result in intraspecific associations rather than interspecific associations among animals occupying similar ecological niches.

Summary

The aggressive behavior of 16 *Peromyscus maniculatus bairdii* and the C57BL/10 inbred strain of 16 *Mus musculus* was measured in individual combats with members of the same species and members of the other species. The *Mus* were more aggressive than *Peromyscus* in both intraspecific and interspecific combats. Patterns of aggressive behavior characteristic for each species tend to be maintained when both species encounter each other. The great aggressiveness of *Mus* suggests that they are capable of driving *Peromyscus* out of natural situations whenever the two species frequently encounter each other.

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A SURPRISING CASE OF SURVIVAL

It is well known that beetles of the families Dryopidae, Elmidae, Parnidae, and Psephenidae are to be found as both larvae and adults on rocks submerged in the riffles of fast-moving streams. One might easily infer from the absence of these forms in slower parts of the streams that they are unable to tolerate some factors such as high water temperatures or reduced levels of dissolved oxygen. By sheer accident the writer observed an impressive demonstration of tolerance by an imago of one of these "riffle beetles" and it is thought that this observation may be of interest to others speculating about the factors that restrict the distribution of these beetles.

On Saturday, April 9, 1955 a class in Animal Ecology was studying a rapid section of Cascadilla Creek at Town Line Road just east of the Cornell campus and of Ithaca, New York. This stream has a typical "torrential" fauna including mayflies, stoneflies, blackflies and an abundance of the "water-penny" larvae of *Psephenus herricki* (DeKay) (= *P. lecontei*). The day was sunny and it was found that if rocks were lifted from the riffles and inverted on the bank they would, as they dried, yield numerous small adult beetles that had been concealed in crevices and depressions. The class collected many of these imagoes and preserved them in alcohol. The writer collected one imago into a shell vial of 20 ml capacity and corked the vial without adding preservative. Three ml of clear water were included in the vial with the beetle.

After the field trip this vial was placed on a desk and forgotten over the week-end. On Monday the writer was surprised to find the beetle alive and active after spending two days at room temperature in a tightly corked vial and he decided to see how long it would survive. Within a week the water in the vial was green with algal growth and it was observed that a small red water mite, probably *Limnochares* sp., was also present along with the beetle. No identifications were attempted as this would have necessitated uncorking the vial.

Subsequently, the vial and the beetle were forgotten for periods of time of varying length. Several times the vial became buried under papers for weeks at a time between examinations. On such occasions the algae turned yellow but the green color always returned after the vial was again exposed to light. The red mite disappeared entirely. The beetle was observed to be active whenever the vial was examined right up until the time of summer recess. Over the summer vial and beetle sat on the desk completely neglected. July and August were exceptionally warm months with the maximum official temperature reaching 98° F in July and the mean daily maximum being 88.8° F. The air temperature in the office containing the beetle was unquestionably above 100° F for several days.

The beetle survived through all this and also through the following winter during which it was again neglected for varying periods of time. It was still alive and active on May 7, 1956 but it was dead when the vial was next examined on May 11, 1956. Thus this beetle had survived submerged in 3 ml of water for a minimum of 394 days during which it had been subjected to much higher temperatures and lower oxygen tensions than would ever occur in natural bodies of water in this region.

The bettle was identified by Dr. Harry G. Nelson of the Chicago Natural History Museum as a female of *Stenelmis crenata* Say. The algae in the vial proved to be an unidentifiable mass of Palmella stages.

The noteworthy things about this accidental observation are that this small beetle, roughly 2 mm in length, has a potential adult longevity of well over one year and that the adult female at least is able to tolerate certain environmental conditions more extreme than would occur in pools, ponds, and puddles. These beetles have access to such habitats and, in fact, must frequently be washed into such places but they do not persist there. We do not know what factors eliminate these beetles from lenitic habitats but it is probable that lethal influences of high temperature and low oxygen tension on the imagoes can be eliminated as possible controlling factors.

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FACTORS LIMITING ROOT PENETRATION IN DEEP SANDS OF THE SOUTHEASTERN COASTAL PLAIN

Root penetration of all species is very shallow on the sandhills of the southeastern Coastal Plain. Fertility of these deep sands is poor, the water-holding capacity is small, and the water table is usually at least 40 or 50 feet below the surface. The vegetation is principally scrub oaks (mainly *Quercus laevis* and *Q. incana*) and wiregrass (*Aristida stricta*), with a scattering of longleaf pine (*Pinus palustris*).

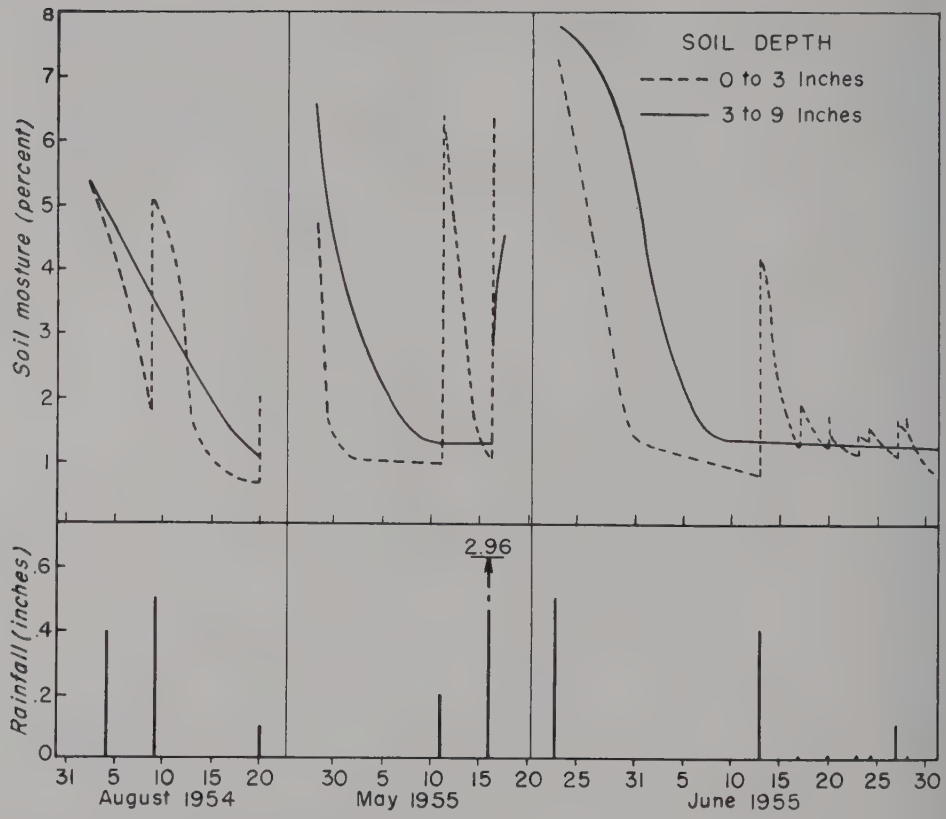

FIG. 1. Rainfall and soil moisture at two soil depths in Lakeland sands in western Florida having ground cover of undisturbed scrub oaks and wiregrass.

Plants of all species form a thick mat of fibrous roots within 4 or 5 inches of the surface. Below this, there are few large roots and almost no small ones. Observations of 4-year-old slash pines (*P. elliottii*) that had been planted on the sandhills near Marianna, Florida, showed that very few roots had penetrated below three inches. This was true of pines planted on denuded spots as well as those on undisturbed scrub oak-wiregrass roughs. Roots that had grown below 3 inches were poorly developed. Mature trees showed a similar distribution of roots.

Heyward (1933), studying longleaf pine in the same general region, found that "approximately 90 percent of all the lateral roots excavated occurred within a foot beneath the surface of the soil." One lateral root was 75 feet long and ran at an avearge depth of 10 inches below the surface for 71.5 feet of its length.

In the deep sands of North Carolina, Wells and Shunk (1931) found that the roots of wiregrass were concentrated in the surface 4 inches of the soil and descended below 1 foot only when the water table was within a few feet of the surface.

Development of superficial root systems seems to result from a combination of moisture, fertility, and biological factors that is somewhat unique to the sandhills.

Rainfall distribution.—Near Marianna, Florida, precipitation was measured daily at two locations for 2 years. Soil moisture, in the local Lakeland series, was determined three times weekly from Colman fiberglas soil unit readings. Data from both sites were averaged.

During the two-year period half of the storms were 0.4 inch or less. Storms as great as 0.4 inch would sometimes wet the 0- to 3-inch soil layer, but this water never penetrated to the 9- to 12-inch depth (Fig. 1). Under such conditions, more root growth would be expected in the 0- to 3-inch layer than in lower ones.

Fertility at lower depths.—Fertility is nearly always very poor in sandhill soils. Even so, the surface 3 inches may have a much greater mineral content than lower layers. In typical Lakeland sands of Florida, nitrogen may be 3 to 4 times more abundant in the upper 3 inches than in the 9- to 12-inch layer (Table I). Calcium may have an 8 to 1 ratio at the same depths.

Wells and Shunk found similar decreases of mineral content in deep sands of the North Carolina Coastal Plain. They suggested that, when soil moisture is below field capacity, competition for limited nutrients does not permit roots to grow to capillary water at lower depths. At the same time, high surface tensions prevent re-equilibration of the interstitial water upward in the profile (1931). Even in the absence of competition, fertility would seem

TABLE I. Properties of Lakeland soils as influenced by depth: averages of five locations[1]

Soil depth (inches)	Organic matter	Total nitrogen	Total exchange capacity	Calcium
	Percent	*Percent*	*m. e./100 gm.*	*m. e./100 gm.*
0 - 1	2.23	0.045	4.0	1.31
2 - 3	1.56	.029	2.6	.51
4 - 5	.60	.018	1.6	.17
8 - 9	.30	.011	1.1	.16
18 - 21	.22	.007	1.1	.16
26 - 42	.19	.008	1.1	.15

[1]Data tabulated from Gammon, N., *et al.* 1953. Physical, spectrographic, and chemical analyses of some virgin Florida soils. Univ. Fla. Agr. Expt. Sta. Bul. 524, 130 pp.

sufficiently poor to retard root growth at lower soil depths.

Winter soil temperatures.—Midday soil temperatures were determined from thermistors in the Colman units, at the same depths, locations, and dates that moisture determinations were made.

In midwinter, the upper 3 inches were often 10°F. warmer than the 9- to 12-inch layer. For example, the average midday temperature on 4 selected days in the winter of 1953-54 was 67° at the 1-½-inch depth; 61° at the 4-½-inch depth; 58° at 7-½ inches; and 56° at depths between 10-½ and 24 inches (Table II).

TABLE II. Noon soil temperatures on selected winter dates at the Chipola Experimental Forest, in degrees Fahrenheit

Soil depth (inches)	DATE			
	December 21, 1953	January 6, 1954	January 20, 1954	February 17, 1954
	Degrees	*Degrees*	*Degrees*	*Degrees*
1 - ½	62	64	70	72
4 - ½	56	58	67	64
7 - ½	52	54	63	62
10 - ½	51	53	61	60
18	51	54	60	60
24	51	54	58	60

Considerable surface development of roots took place during the winter. Succulent white new growth, often ¾-inch long, was found on the excavated roots of pines and wiregrass in December and January. High winter temperatures in the surface 3 inches of the soil apparently stimulated root development in this layer.

Maximum summer soil temperature at the 1-½-inch depth was 113°F., but usually the daily maxima were 100° or less. Lower depths were always cooler than the upper layer. Despite occasional high temperatures, extensive root development was observed.

Decomposition of soil organic matter.—Organic matter in sandhills is concentrated in the top 4 or 5 inches; below this depth, there is hardly enough to detect visually. Some of the organic matter comes from surface litter, but most of it seems to be derived from dead wiregrass roots. These observations are supported by the findings of Wells and Shunk.

Even though the instantaneous rate of biological activity in sandhills soils is relatively low, the yearly cumulative total is fairly large, chiefly because the high winter soil temperatures permit activity throughout the year. Heyward (1937) found that only 10 to 15 years are required to establish a stable climax soil profile in the longleaf pine type. This also may be the case in the oak-wiregrass type on the same soil series. Organic matter in the upper soil horizons is completely decomposed before it can be washed to lower horizons, a circumstance that prevents formation of a progressively deeper topsoil.

The organic matter in the surface 3 inches has a pronounced effect on exchange capacity (Table I): the greater the organic content, the more favorable the mineral-retaining capacity. This means, once again, that conditions are more favorable for growth in the upper few inches of soil, and that surface development of roots is encouraged.

It is not proposed that all 4 of these mechanisms function all of the time. It is their combined and recurrent action that probably restricts roots in deep sands to the surface layer.

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RAPID METHOD FOR THE DETERMINATION OF CARBON DIOXIDE EVOLVED FROM FOREST SOILS[1]

For more than a half century, the evolution of carbon dioxide has served as a measurable manifestation of the life processes which take place in the body of the soil. A detailed review of soil respiration studies is given in the comprehensive text of Lundegårdh (1954). Although the evolution of carbon dioxide has been largely investigated in farm soils (Russell, 1950, p. 337), it may have a greater practical significance in silviculture. In recent times, foresters have been using heavy applications of toxic biocidic compounds whose adverse effect on soil organisms and roots of trees may be detected by respiration analyses. The analysis may reveal the alteration in the microbiological activity of soils resulting from different methods and intensities of silvicultural cuttings. Application of fertilizers, preparation of composts, deleterious effect of burning, and appraisal of forest humus are among other phases of forestry practice in which the

[1] Contribution from the Soils Department, Wisconsin Agricultural Experiment Station in cooperation with the Wisconsin Conservation Department. Publication approved by the Director of the Wisconsin Agricultural Experiment Station.

determination of carbon dioxide evolution may prove of value.

The difficulties which have precluded in the past extensive determination of carbon dioxide evolution are twofold: unreliability of results obtained with samples of humus or soil analyzed under artificial laboratory conditions; complicated techniques of field analysis, as used for example by Romell (1922). Fortunately, the recent manufacture of small battery-operated vacuum pumps has made it possible to assemble a portable unit for simple and rapid determination *in situ* of carbon dioxide evolved from soil. The construction of the apparatus (Fig. 1) and the results obtained under different soil-forest conditions are described in this note.

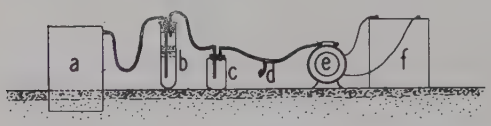

FIG. 1. Apparatus for the rapid determination of carbon dioxide evolved from soil: (a) metal cylinder, 5 inches in diameter; (b) test tube with a capillary inlet to regulate the bubbling of air through the sodium hydoxide solution; (c) safety bottle to prevent the accidental flow of liquid to the vacuum pump; (d) "T" valve to control the air flow; (e) Trico "Electro Vac" pump; (f) Six-volt storage battery.

The air is extracted from the soil through five-inch diameter glass funnels or metal cylinders (a). The use of metal cylinders is particularly desirable in soils covered with raw humus. The funnels or cylinders are firmly embedded in the soil and the air is drawn through rubber tubing provided with capillary tips. The carbon dioxide is trapped in a normal solution of sodium hydroxide placed in the test tubes (b). The air suction is accomplished by a Trico "Eletcro Vac" pump (e) operated by a six volt storage battery (f). The rate of air flow is controlled by a "T" valve (d) placed in the line between the pump and the safety bottle (c). To facilitate transportation, the entire assembly with the exception of the battery is accommodated in a wooden rack.

Originally an attempt was made to regulate the passage of the air through the sodium hydroxide solution at a rate of one bubble per second. Later it was found that the insertion of the capillary tubing, controlling bubble size, eliminates the need for adjustment of the air flow. The capacity of a fully charged battery is six hours of uninterrupted operation. To reduce the need for frequent recharging, the six volt assembly may be replaced by a twelve volt unit, which has now been placed on the market. Experience has shown that a two-hour period is ample for extracting a volume of air sufficient to assure reliable results. The quantity of carbon dioxide extracted from the soil at different intervals is graphically presented in Figure 2.

The NaOH, converted in part by carbon dioxide into Na_2CO_3, is treated with an excess of 2 *N* BaCl and titrated with *N* HCl. The original volume of NaOH minus ml. of titration gives the volume of NaOH converted to carbonate. The total number of ml. of converted NaOH times 0.022 g. gives the grams of the evolved carbon dioxide. The results are usually expressed on a square meter basis using the formula

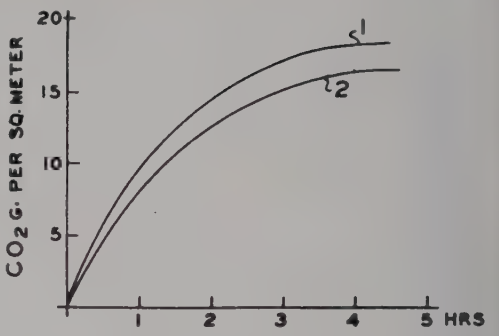

FIG. 2. The content of carbon dioxide evolved from soils supporting a cover of orchard grass (1), and a stand of red and black oak (2) as determined at different time intervals. Note the equi-distance of curves after a two-hour period.

$$CO_2 \cdot \frac{10{,}000}{r^2}$$

where r is the radius of the funnel or cylinder in centimeters.

One six-volt unit can operate as many as sixteen funnels spread over an area of one-twentieth of an acre. This number of duplicates provides sufficient data for statistical analysis. Because the evolution of carbon dioxide is influenced by atmospheric conditions, the analysis is performed by two units placed in representative parts of the study area and operated simultaneously. If desired, the carbon dioxide content of the air is determined by placing a pair of funnels above the ground (Fig. 3).

FIG. 3. Determination of carbon dioxide utilizing six sampling funnels for soil and two for air analysis. Note the carrying rack accommodating the test tubes, funnels, and the vacuum pump.

The applicability of the method is illustrated by the results obtained under different soil-forest conditions during the month of August (Table I).

The results of both series of soil analyses performed in the sodded area, hardwood stand, and the pine plantation, University of Wisconsin Arboretum, show clearly the differences in the respiration effected by the vegetative cover.

Analyses of soils in the virgin hemlock-yellow birch stand at the Sweeney Lake Timber Reserve, Oneida County, Wisconsin, and adjacent area occupied by a blue

TABLE I. Amount of carbon dioxide evolved from soils under the influence of different vegetative cover and fertilizing materials

Soils analyzed	CARBON DIOXIDE, G./SQ. METER/HOUR				
	Determinations				Average
	1	2	3	4	
Nut-structured silt loam supporting a fully stocked stand of red and black oak, 90 years old	7.26	7.81	7.97	7.97	7.75
Similar soil supporting fully stocked red pine plantation, 25 years old	4.35	3.09	4.13	3.25	3.70
Soil of an adjacent area under cover of orchard grass	8.84	8.13	8.68	9.54	8.80
Nut-structured silt loam supporting a fully stocked stand of red and black oak, 90 years old	4.51	4.39	4.88	4.69	4.62
Similar soil supporting fully stocked red pine plantation, 25 years old	3.92	4.13	3.21	3.23	3.62
Soil of an adjacent area under cover of orchard grass	5.21	6.42	6.25	6.60	6.12
Podzolized fine sandy loam supporting a virgin stand of hemlock and yellow birch	2.78	3.12	3.12	3.47	3.12
Similar soil sterilized by blue heron excrements (rookery area)	0.61	2.06	2.18	0.56	1.35
Non-podzolic soil of glacial outwash supporting cover of quack grass	2.76	2.92	3.16	2.92	2.94
Adjacent area top-dressed with fermenting sawdust compost	23.28	22.25	22.25	19.96	21.94

heron rookery are of considerable interest. They conspicuously reveal the sterilizing effect produced by an unreasonably high concentration of birds with resulting accumulation of toxic ammoniated by-products.

Finally, the observations made on worn out outwash sand in the vicinity of the Griffith State Forest Nursery, Wisconsin, strikingly illustrate the rejuvenating effect on microbiological activity of soil produced by the application of fermented sawdust compost.

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FURTHER DATA ON THE RATE OF ORGANIC MATTER ACCUMULATION IN BOGS

The writer reported (Leisman, 1953) on a study of the rate of organic matter accumulation on the sedge mat zones of bogs in the Itasca State Park region of Minnesota. This study involved the use of tamarack seedlings as an index of the rate of peat accumulation. In brief, the depth of accumulation around each seedling was measured from the surface level of the sedge mat down to the cotyledons or cotyledon scars, and the depth of peat divided by the age of the seedling to ascertain the annual accumulation rate. The position of the cotyledons in relation to the surface level at germination was ascertained by examination of current year seedlings.

A total of seven bogs was studied in this manner, and a fairly constant rate of 0.59 inch (1.50 cm) per year for at least the first six to eight years of accumulation was obtained. One of the best bogs in this study was Twin Lakes F, where a large number of seedlings was available for measurement. The location and description of this bog was given by Leisman (1953). The calculated rate of organic matter accumulation on the sedge mat by measurement of the seedlings was 0.54 inch (1.37 cm) per year. At the conclusion of the field work in August, 1951, the writer laid down a 17 foot length of insulated wire flush on the surface of this sedge mat in the same area where the seedlings were taken. This was done in the hope of visiting the bog sometime in the future and measuring the depth to which it had been buried, thus checking, at least partially, the validity of this seedling method.

This opportunity was presented in August, 1955, and the writer was able to locate and measure the burial depth of the wire. Measurements were taken from the surface level of the peat down to the lower edge of the wire at one foot intervals along the entire length of the wire. The depth of burial ranged from 1.5 inches (3.8 cm) to 3.0 inches (7.6 cm). A total of 18 measurements gave a sum total of 40.25 inches (102.24 cm). This total of 40.25 inches divided by the total number of measurements, 18, gave an average depth of burial for the wire of 2.24 inches (5.69 cm). This average divided by the number of years elapsed, four, yielded an average rate of burial or, in other words, an average rate of organic matter accumulation of 0.55 inch (1.40 cm) per year.

A comparison of this rate with that calculated by the seedling method (0.54 inch per year) indicates a remarkable agreement. While it would be ridiculous to assume that this single instance of agreement entirely validates the seedling method, the writer none-the-less believes that this indicates that the use of tree seedlings on sedge mat zones of bogs gives a reasonably accurate measurement of the rate of organic matter accumulation.

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REVIEWS

The North American Grassland in Historical Perspective[1]

A comprehensive survey of grasslands research and a reassessment of the status of American thought about grasslands at midcentury is long overdue. The book under review by John E. Weaver and F. W. Albertson,[1] and the earlier book by Weaver,[2] although important events under the first category, do not qualify for so important a dual role. The retirement of Dr. Weaver from the post he has held so long at the University of Nebraska has afforded him, aided by others who look to him as mentor, to sum up a life time of research and teaching. Although the core of both books is the studies of these men, the volumes include some research, the basis of choice being highly selective, from outside the Nebraska school of ecology. The area covered by the two volumes is the grasslands of North America lying between the forest lands of the eastern side of the continent and the Rocky Mountains—the great interior of the North American continent. The eastern part is designated as the True Prairie and is described in the earlier Weaver book. The western part, called the Mixed Prairie, is the subject of the Weaver and Albertson volume, the part which "lies almost entirely in the Great Plains." But in the process of differentiating the Mixed and the True Prairies, a third area emerges, a transition country about 50 miles wide (p. 18). Of course, such a third division, only usually indicated as wider, was first delineated by mid-nineteenth century travelers and explorers who described the landscape of the mid-latitudes, and was insisted upon as an ecological division by J. H. Schaffner,[3] but has not been a part of the several related strains (Clements, Weaver, Shantz-USDA) of ecological traditions.

The sequence of chapters in the book is truly puzzling. Chapter 1 is mostly definitions; chapters 2-3 describe the Mixed Prairie; chapter 4 describes the vegetation of western Kansas as an area; chapters 5-10 inclusive report the effects upon the central Plains vegetation of the drouth of the 1930s and the wet years of the 1940s; chapters 11-12 resume the areal descriptions, dealing with the Sand Hills of Nebraska and the adjoining Plains; chapter 13 describes generally the Plains plants underground; chapters 14-21 inclusive resume the areal descriptions of vegetation by states or the Mixed Prairie parts thereof, Colorado, Oklahoma, Texas, New Mexico, North Dakota, South Dakota, Montana and Wyoming together, and the Canadian prairies. The final chapter describes the non-grasses. A note should be made of the fact that the chapter on Texas is written by B. W. Allred, and the one on New Mexico by Arnold Heerwagen. The most of the book is factual reporting upon research items rather than an over-all synthesis. A striking aspect of the research reported upon is its short-term character, the number seven turning up rather frequently as indicating the longer-term studies.

In view of the wording of the sub-title, which includes the "nature" of grasslands, and the statement in the preface that: "This great prairie land has been thoroughly examined as to its way of life both above ground and deep in the soil. . . ." this reviewer has a "concern" about omissions; first, those of strictly ecological nature—temperature fluctuations, and the light, altitude, and genetic factors, animal ecology, and the relations of animals and wind to soil movement and to soil formation; all essential to the "nature" of the grasslands even from the standpoint of the plant ecologist in the strict application of that term. Although mentioned, the authors do not come to grips with the role of fire. The second category of omissions or inadequate treatments is historical in character.

Major aspects of this grass book are based upon facts and assumptions about facts that are historical in character. In introducing at all the subject of the historical origin of the Great Plains or of the High Plains portion, and of the grasses, and in drawing theoretical assumptions from that history, the authors incurred an obligation to achieve a reasonable approximation of adequacy. In this perspective a historian long interested in grassland ecology has something to say that lies peculiarly in his province. Geological history and paleobotanical beginnings are only vaguely sketched, leaving gaps especially serious in the period of transition between late Pleistocene time when only geological records are available, and time recorded also in written documents. As late as 1930, anthropologists were convinced that no human culture occupied the Great Plains prior to the American Indian known to European invaders. All that has changed. Primitive man of the Folsom cultural level and more recent has been present continuously or intermittently in the whole or parts of the area for at least 10,000 years. Space does not permit detailed citation of several studies in Pleistocene geology, archeology, and history based on written documents, but the net conclusions are inescapable. Instead of the stability once thought to have prevailed in the Great Plains the record has revealed great instability. The geological record of erosion by water and wind, and redisposition of material is highly complex. Individual sites show successive occupances evidenced by layered deposits. Those layers containing evidence of human occupance are separated from each other by thick coverings of windblown material indicating long periods of dust blowing, without vegetation, during which the sites appear to have been abandoned. Within the period of written record, Isaac McCoy's journal of a surveying expedition of 1830, in what is now north central Kansas, recorded dust storms so dense as to blot out the sun. The present reviewer's compilation of dust storm records 1850-1900 shows repeated periods of dust blowing in areas yet unoccupied by white men or only partially settled. Recent studies of the migrations of Indians from the forested area into the Great Plains, of buffalo movements, and of the introduction of the horse, all since the coming of the white man, require substantial revision, if not abandonment, of the traitional views about a cultural equilibrium between the Indian and his environment. Instead of the assumption that the Great Plains had not been disturbed prior to the coming of white men, it might be nearer the truth to say that no major part of the area has escaped disturbance by both natural phenomena and primitive man.

[1] Weaver, J. E. and Albertson, F. W. 1956. Grasslands of the Great Plains. ix + 395 pp., illus. Lincoln, Nebraska: Johnsen Publ. Co. $6.50.

[2] Weaver, J. E. 1954. North American Prairie. xi + 248 pp., 87 fig. Lincoln, Nebraska: Johnsen Publ. Co.

[3] Schaffner, J. H. 1926. Observations on the grasslands of the central United States. Ohio State Univ. Studies, Contributions to Botany no. 178: 1-56.

In this historical perspective there is legitimate ground to question whether the facts presented in these research studies reported upon by Weaver and Albertson substantiate the theoretical assumptions which control their interpretation—the predominant climate succession-climax concept and the consequent range management objectives. A case in point is the citation (p. 22) of how Clements discovered the alleged true character of Great Plains vegetation as a Mixed Prairie climax—the investigation of 1915 during an excessively wet season. Similarly, an excessively dry sequence would have afforded "proof" of the opposite. Climax of what? Upon what authority are excessively wet seasons adopted as the true measure of Great Plains climate? Excessively dry seasons are fully as characteristic of that climate. Also, the historical evidence seems conclusive that some areas were completely denuded of vegetation, not once, but repeatedly, and within relatively recent time—historical time in the conventional sense as contrasted with geological time. Soil was blown or washed away from some spots and accumulated at others. On occasion prairie dogs, for example, denuded large areas and their burrowings disturbed the soil. Whether destroyed or drastically damaged by wind, water, or animals, vegetation was obliged to make a new or virtually new start on disordered soil. The facts would seem to emphasize the importance of dealing with each spot in terms of what is actually present at a particular time. A vegetation map must be dated. But, in any case, extreme emphasis upon water relations is unreal as so many factors are involved in the vegetation-forming equation. Temperature fluctuations are associated with the shifting of particular types of vegetation north or south. Intensity of light is variable. Altitude and photoperiodism of specified points are as constant as factors can be, but plant responses vary and affect distribution. The role of variant genetic composition within recognized species is little understood in its ecological relations. But these matters do not appear in the book under review.

This book and its companion volume may be regarded as recording the end of an era, the formative period of approximately a half century of ecology in the United States. Already, however, the Classical schools of American ecology, that looked to F. E. Clements, and to H. C. Cowles, have been largely superseded. This conclusion is not intended to depreciate their importance. They were the pioneers who blazed the trail when the going was hard. The product of their labor in the accumulation of ecological facts will survive the obsolescence of their theory. In the second half of the twentieth century the new ecology is in the hands of new men with highly diverse backgrounds of training. Several disciplines now converge upon ecological problems, and the setting up of one-man systems for the whole field is extremely difficult, if not impossible. These new men with their varied approaches have the opportunity to do better than the pioneers, but that is no guarantee that they may not do worse with the heritage at their disposal.

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Gradient Analysis in Agricultural Ecology[1]

One of the major developments in ecology during the past decade has been the growth of applied plant sociology in Europe. From Continental phytosociology, traditionally oriented toward classification and description of natural communities, a number of effective approaches to the application of synecological knowledge for better use of the land by man have emerged. The three small volumes of Ellenberg's Agricultural Phytosociology are an outstanding example of this development.

The first volume considers Weed Communities as Indicators of Climate and Soil; the emphasis is on the manner in which the weed stand of a farm field expresses, in its whole floristic composition, the whole environmental complex of that field. Weed communities of the long-cultivated fields of Europe have come to a degree of equilibrium with environment; they are by no means accidental assemblages. Not only may weed community-types express environment; weed stands may be quantitatively analyzed for indication of various site factors.

For study of soil acidity, community samples from different fields were arranged in an ecological series, from low to high pH values. Species were grouped by their distributional relations in this ecological series, or synthetic transect, into six classes—from 1 (predominantly on strongly acid soils) to 5 (predominantly on neutral or alkaline soils) and 0 (with wide amplitude and hence valueless as an indicator for this factor). The numbers from 1 to 5 are "reaction-numbers" expressing the indicator meaning of species in relation to soil acidity. When reaction-numbers for all species in a weed stand are added together, and divided by the total number of species (exclusive of class 0), a "mean reaction-number" results which combines the indicator information offered by the various species. Significant correlations can be shown between these mean reaction-numbers and mean pH values for soil. The mean reaction-number is thus a quantitative indicator, expressing relative positions of weed stands and the soils they occupy along the soil acidity gradient. This approach to quantitative indication through weighted averages is basically the same as that used in this country for moisture relations, especially, of more natural vegetation; a number of authors have discovered the technique independently.

The same species classified by soil acidity can be classified by relations to other gradients and factors, proceeding from those which are best known to those less well understood. Species were classified by moisture relations; and mean water-economy numbers for stands were derived as indicators of certain aspects of soil structure and moisture conditions. Species were grouped also by their relations to soil nitrogen, temperature rela-

[1] Ellenberg, Heinz. 1950-54. Landwirtschaftliche Pflanzensoziologie. Stuttgart: Eugen Ulmer.

Band I. Unkrautgemeinschaften als Zeiger für Klima und Boden. 1950. 141 pp., 23 figs., 19 tables. DM 6.80, $1.65.

Band II. Wiesen und Weiden und ihre standörtliche Bewertung. 1952. 143 pp., 23 figs., 26 tables. DM 6.80, $1.65.

Band III. Naturgemässe Anbauplanung, Melioration und Landespflege. 1954. 109 pp., 30 figs., 19 tables. DM 6.—, $1.45.

tions according to northern boundaries, and continentality by east-west distribution. A single weed species is by itself almost worthless as an indicator; but considered together with others, as part of the total community composition, each species may contribute information on each of the environmental gradients studied. The various edaphic and climatic gradients, together, form a multi-dimensional field in relation to which species and communities are studied. Composition of a given stand, analyzed from various standpoints according to distributional relations of its species to different major factors, provides a useful, though not exact, indication of the stand's position in relation to each of the factors studied.

Each plant species makes specific demands on its environment; no two species are alike in ecological relations. Species which resemble one another in their relations to major factors, however, can be assembled into "ecological groups"; 25 such groups were recognized among the weed species. Many species could not be assigned to them, and each group is necessarily an abstraction from the individuality of plants. The ecological groups are distributed, somewhat independently of each other, into stands in various combinations. Of the many possible combinations, those most frequently realized are the community-types recognized. The essential distinction between community and community-type is made by Ellenberg through the terms *Pflanzengemeinschaft* and *Pflanzengesellschaft*. The approach through ecological groups is considered a useful adjunct to, but not a substitute for, classification in the manner of Braun-Blanquet and Tüxen. Ellenberg indicates his acceptance of the system of Braun-Blanquet in this work, though he has expressed significant reservations elsewhere.[2]

This book may be an eye-opener to any ecologist who regards weeds less as sources of ecological information than as vegetational static, who disguises a scorn for such plants by a fancy term, "ruderal." The significance of Ellenberg's work goes beyond his remarkable demonstration of the ecological significance of these unimpressive communities, however. His book is both an admirable exposition and a successful application of the approach to vegetation through analyzing distributional relations of species and correlating gradients of community composition with gradients of environment—the approach of "gradient analysis" or "ordination." The convergence—in concepts, techniques, and perspective—with such work in this country[3] is striking, and the more striking because it is a convergence from the very different backgrounds of American ecology with its emphasis of dominance, the school of Braun-Blanquet with its emphasis of floristic composition, from such very different applications as to American forest communities, and the weeds of farm fields in Germany.

The second volume, on meadows and pastures and the evaluation of their sites, develops the same approach to grassland communities. Relations of grassland species and communities to moisture conditions, soil pH, nitrogen content, temperature, light, and various management practices, are considered. On the classification of these communities, Ellenberg observes that European experience shows dominance-types to be weak indicators of environments; classification must be based on total floristic composition, approached either through ecological groups or through character-species and differential-species in the system of Braun-Blanquet. Grassland community-types (alliances) of the latter system are arranged in a multi-dimensional pattern according to three major axes —moisture relations, acidity, and nutrient relations. The third volume deals with the planning of land use in accordance with the natural potentialities of the land, and the care of the land. Problems of erosion and wise use of various kinds of landscapes discussed, and uses of vegetation mapping, treated also in the first two volumes, are developed further. Problems of conservation are considered only for Germany; but the discussion is notable for the author's insistence on the need for avoiding facile generalizations and one-sided evaluations, for recognizing and dealing with the real complexities of natural communities and their environments—the diversity of communities and land-use problems covered by the term "moor" for example.

Applied ecology must often depend upon what has already been done in basic ecology, contributing techniques to the latter, but usually not fundamental concepts and methods. Ellenberg's work is an example of the reverse relation, which also is possible; for useful concepts and an important method have been contributed to the main phytosociological tradition from work which is applied, but also basic research. His books on agricultural phytosociology deserve thoughtful study by ecologists from the standpoints of both applied ecology and the basic understanding of communities and methods for their study.

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[2] Angew. Pflanzensoz. [Wien], Festschr. Aichinger 1: 134-143, 1954.

[3] Curtis, J. T. Ecology 36: 558-566, 1955, Whittaker, R. H., Ecol. Monog. 26: 1-80, 1956, and work cited therein.

Two New European Commentaries on Phytosociology

Two books have recently appeared, one in French[1] and the other in Italian,[2] which contain re-statements of the "Montpellier doctrine" and at the same time give some consideration to the thought and accomplishments of other schools. Both Guinochet and Tomaselli have been somewhat influenced by American experiments, but from very different standpoints: the developments of biosystematics and especially the work of Edgar Anderson and G. L. Stebbins are taken into account by Guinochet, whereas Tomaselli has remained nearer to the core of the subject by incorporating Clementsian and post-Clementsian dynamics. A summary of these two important works will

[1] Guinochet, Marcel. 1955. Logique et dynamique du peuplement végétal. Phytogéographie. Phytosociologie. Biosystématique. Applications agronomiques. Paris: Masson (Collection "Évolution des Sciences," No. 7.) 143 pp., 32 figs., 4 plates. 880 fr., $2.55.

[2] Tomaselli, Ruggero. 1956. Introduzione allo studio della fitosociologia. Metodi di studio della vegetazione ad uso scientifico, agricolo e forestale. 319 pp., 30 tables, 70 figs. Milan: Industria Poligrafica Lombarda. 4000 lira, $6.40.

be given herewith as well as an assessment of the above-mentioned crosscurrents and a critical evaluation of the syntheses offered by the authors.

Guinochet closely follows the French tradition of keeping hypotheses in sight and as such, and does not take as much for granted in the field of evolution as most Anglo-Saxon writers are currently doing. Nevertheless, the whole perspective of his book is evolutionary and does not very significantly depart from the views of Simpson, Dobzhansky, Huxley, or Stebbins. He belongs to a very small group of Frenchmen who, in the thirties, opposed "official" views on the potential contributions of cytogenetics to biological theory. Possibly, among these, he was then the only one to attempt a bridging of the large gap between genetics and ecology. Through the years he has made many contributions to both and now attempts a general review of environmental adjustments.

The first three chapters concern the organic diversity of the plant world and the problems of centres of origin and dispersal. He draws very exhaustively from the work of Emberger and also somewhat from Gaussen (both of whom are too little known on this side of the Atlantic) for a unified phylogenetic scheme. The latter, however, is not in any detail referred to environmental changes. On the contrary, origin and migration, in a more recent sense and involving much smaller taxonomic units, are illustrated from the examples provided by the Scandinavian and American workers, and many of Cain, Anderson, and Stebbins' interpretations are brought forth. The part on floristic territories is rather weak, by comparison, and the generalities of Emberger's "floristic empires" do not relate very clearly to subsequent considerations on the genesis of floras. The essentially historical premises of floristics are not well defined and allow some confusion later on between taxonomic-evolutionary and vegetational criteria in the delimitation of "natural areas."

The fourth chapter contains one of the very best accounts in French of current ideas on plant populations. Many of the actual examples are taken from the work of Edgar Anderson and his students and many quotations are translated from G. L. Stebbins in the statements of general principle and theoretical reasoning.

Chapter five is one of the most substantial and original in the whole book, as it brings the Montpellier phytosociological concepts into the focus of the evolutionary processes previously reviewed. It may very well be that this School is, in a very real sense, more congenial to an integration of the acquisitions of biosystematics than other more "ecological" approaches. Resting as it does almost exclusively upon "presence-absence of species" (p. 65), it emphasizes the floristic criterion to the extreme and therefore possibly the historical determinism of the species rather than its present, immediate, and, possibly, ephemeral limitations. Thus the evolutionary instead of the ecological argument is best served, for instance in cases such as that of the rosemary-rockrose association "with and without pine cover." I feel quite sure no North American vegetation student would be willing to consider these two sites and communities as similar.

Guinochet goes on, in this same chapter, to define the phytosociological concepts and methodology and presents several applications. In chapters six and seven, the physical elements and dynamics are drawn into the picture, but as it seems, *a posteriori*. It does seem, from a consideration of much continental phytosociological work (from North Germany to Portugal and from Poland to Algeria), that knowledge of physical factors and of dynamic sequences in no way orients the investigation.

Chapters eight, nine and ten refer to the "significance and causality of plant associations," to the "contributions of phytosociology to the knowledge of species" and to the "concepts of individual, populations, species and association." The author concludes (p. 126) that "as an individual-organism corresponds to a characteristic combination of genes, thus an individual-community corresponds to a characteristic combination of species." This analogy is much disputed, of course, and must be accepted or rejected on philosophical rather than scientific grounds.

The final chapter reviews practical applications to silviculture, flood control, agriculture, etc., and also claims that phytosociology provides a good introduction to "operational research."

One could wish for a more substantial bibliography: only twelve titles are given at the beginning of the book; the footnotes add a few more. But many authors are referred to without citation. The illustrations are excellent, well printed and well placed in the text.

There is a great deal of food for thought in this slender volume. Although a few chapters are somewhat weak and although various phases of the subject are omitted (e.g. tropical and arctic research), it develops a unified argument and, as such, is a valuable contribution to a synthesis of evolutionary and ecological progress.

Tomaselli is probably the most authentic representative of the Montpellier School in Italy, of what he himself calls the "sigmatist current."[3] In fact, the implantation in his country of the Braun-Blanquet methodology has always met with sharp opposition, as witness the very long-winded plea by the dean of Italian geobotanists, Professor Giovanni Negri.[4] Fortunately this entails no tiresome "chip-on-the-shoulder" literature on the part of the author who makes his statements very straightforwardly.

The first part is an historical account of the emergence of phytosociology, from Humboldt to Flahaut and Schröter to Pavillard and finally to Braun-Blanquet. Here the criteria developed and applied at the SIGMA and the scales which it has used to make its relevés are briefly defined and tabulated. The hierarchy of communities is also outlined. As for the dynamics, the qualifications of Gaussen, Moor, Dansereau are further incorporated to Braun-Blanquet's earlier acceptance of Clements' basic postulate of climax convergence. In the mainstream of sigmatism, Tomaselli recognizes three "schools": Tüxen's in Stolzenau, Emberger's in Montpellier and Conard's in Iowa (teutonically spelled Jowa).

The second part reviews other phytosociological schools and other brands of phytogeography with special reference to their influence upon sigmatism. The conclusions of this chapter probe the question of the relative validity of the approach and in what respects the School might amend its methodology in answer to the criticisms it has undergone. The author offers some of his own research as evidence of a shift towards a more ecological integration.

The third part contains a very useful and graphic pres-

[3] J. Braun-Blanquet has been the director, since its foundation, of the Station Internationale de Géobotanique Méditerranéenne et Alpine, at Montpellier. Therefore, many Europeans and some Americans (e.g. Frank Egler) have for many years spoken of "sigmatism" as it becomes increasingly evident that Zürich and Montpellier are diverging.

[4] Giovanni Negri. Interpretazione individualistica del paesaggio vegetale. Nuov. Giorn. Bot. Ital., n.s. 61 (4): 579-694. 1954 (issued 1956).

entation of surveying methods. These are drawn from many parts of the world and illustrate the fact that much of the Montpellier procedure remains compatible with an ecological "philosophy" which may be very much at variance with that of the School. (Many of us in North America have long been convinced of this.)

The fourth part offers a number of examples of phytosociological studies. It samples different kinds of environment (pastures, fields, bogs, rocky outcrops, forests) and reports well documented studies that show the relation of vegetation to site and to climate. The fifth part covers applied phytosociology and gives prominence to cartography.

The book is paper-bound, printed on good paper, although the illustrations from photographs are not all very sharp. The numerous tables constitute a most valuable documentation and may be readily used for comparative purposes. The bibliography is extensive and inclusive (several misprints in foreign titles) and text references are made easier by appropriate subtitles. Altogether this is a very lively and readable book, its presentation clear, its purpose honestly in evidence.

These two books offer valuable contributions to vegetation study. If they are argumentative in part, we can hardly hold that against the authors, who do not seek to avoid controversy and who have attempted the difficult task of reviewing a broad field of science and to maintain its unity throughout while at the same time incorporating much recent thought and research. It is to be hoped that enough interest can be stimulated to inspire English translations.

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The Study of Plant Communities[1]

Professor Oosting in 1948 presented a new book in plant ecology. This was The Study of Plant Communities, which was offered as an introductory text. In it, community relations were given primary consideration. The book was a timely presentation since it was, besides Professor Daubenmire's text of autecology, the only other first-edition work to become available in many years.

In 1956, Plant Communities was printed in the second edition. This version in its general plan is similar to its predecessor. Using the original format, Professor Oosting revises and enlarges upon his subject material in varying degree. Current developments have been included for a more up-to-date discussion. A selective list of papers from the recent literature is assembled in an expanded bibliography. There are 158 new titles mostly of American works. Eight figures and one table have been added also.

Like the first edition, the revision has the same professed objectives, mainly, of serving as an introduction to the field of plant ecology. The introductory chapter is a consideration of the development and scope of the subject, and of its interrelations with other fields. The presentation then begins with a discussion of the community as an interpretive unit in vegetational analysis, and the subject of measurement and characterization. Considerable attention is given to the study of communities and the criteria used in defining them. Plotless sampling, dispersion types, and a physiognomic classification have been added for a more inclusive presentation. A brief mention is made of ecotypes. It seems this might have been expanded to include a discussion of the implications of ecology, taxonomy, and genetics in population variability and therefore the intrinsic nature of communities.

The chapters on environment have been modified variably by rearrangement and added material. The author draws a perspective of the ecosystem, in which, while vegetation represents a sum product, the study of environmental control is more or less limited to an individual factor basis. The discussion of environmental factors provides a lucidly drawn appraisal of measurements and effects. Added or expanded information includes evaluation of water losses from watersheds, and the measurement of the microenvironment. In the section dealing with temperature, Hopkin's Bioclimatic Law perhaps might have been included as additional background information, as well as an enumeration of Merriam's Life Zones for historical interest. A brief reference to the latter, however, occurs elsewhere in the book. The soil factor previously discussed under one chapter has been reoriented into two, dealing first with origins and formation, and then with ecologic relationships. For the most part the chapter on biotic relations is similar, although some inclusions and modifications were made.

The principal revisions of the book occur in the treatment of succession and climax. In rewriting this section, the author refers to causal factors and the possible variability in successional patterns. Attention is focused on the importance of local circumstances and fortuitous biotic events as causal factors under special conditions. Thus, while trends may be predictable in terms of the general potential, broad explanations are sometimes inadequate, and intensive studies become necessary. The viewpoint of climax interpretation is expanded considerably. The writer presents a critical discourse, and draws upon a wide bibliography, both historical and current, for a lucid and informative discussion.

In the chapter dealing with regional climaxes, an effective orientation is given in North American forms of vegetation. This is generally a duplication of the earlier work, except for some amendments, particularly to desert classification. Following the presentation of current distributions the author proceeds to vegetations of the past, and the various methods of elucidation. A short section on radiocarbon dating is added. There is a chapter on application of ecological knowledge in human affairs, and with this the author brings his presentation to a close.

Perhaps, it would be impossible to write a general text book which in point of content, emphasis, and organization is wholly satisfactory to all readers. In rewriting The Study of Plant Communities, the author aims to provide a perspective of the field as seen primarily through community relationships and problems of study. To this end, the author is largely successful. The text

[1] Oosting, H. J. 1956. The study of plant communities. An introduction to plant ecology. 2nd edn. San Francisco: W. H. Freeman. viii + 440 pp., 198 figs., 12 tables. $6.00.

is clearly written and is amply supported by illustrative material. Generally, the book should prove useful as a beginning text in most areas.

The relative effect of the second edition is considered not as great as that of its forerunner when it was first published. Considering the up-to-date additions and other modifications in subject matter which have been made, the second edition of PLANT COMMUNITIES represents an important contribution as a text in this field of study.

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TWO BOOKS ON BIOSYSTEMATICS AND EVOLUTION IN PLANTS

The impact of genetics and experimental taxonomy upon research in plant ecology is still only gradually and belatedly being felt. Were it otherwise, it would not be difficult to envision the possible effects that current concepts of variation, breeding systems, and evolution in natural populations would have had upon the development of American plant ecology. There can be no doubt, at least, that the currently growing cadre of ecologists who have accepted the individualistic concept of the community have been influenced by the techniques and concepts born during the current renaissance in plant taxonomy, variously called biosystematy, experimental taxonomy, omega taxonomy, etc. The two books reviewed here can be considered respectively as a primer and an indispensable reference work for developing an awareness of the significance of population genetics and experimental taxonomy to all phases of plant ecology.

For a brief summary of the field of biosystematy, the reader is offered the précis by Heslop-Harrison.[1] In 135 pages he is treated to a lucid, elementary exposition of many of the concepts, often concisely illustrated by diagrams and examples, that have resulted from the synthesis of facts from several botanical disciplines. This synthesis, the prime *modus operandi* of biosystematy, is portrayed in the Heslop-Harrison book in a number of ways. The liaison between ecology and taxonomy and genetics that established the field of genecology is given ample exposition. Likewise the fruitful fusions of cytogenetics and taxonomy are adequately summarized.

The little book opens with an essay on the interrelations of classical taxonomy, modern approaches to evolution, and experimental study of variation. This is followed by four chapters on the analysis of variation in natural populations as influenced by ecological factors as well as geographic and reproductive isolation. The concepts of ecotype and cline that have been so expertly extended by British botanists since their first delineation by Turreson and Huxley are given ample airing. Most of the examples illustrating the ecotype concept are from the British literature, a source which has considerably modified the earlier, more rigid, "type" treatment of genecological variation. The chapters on the analysis of variation, however, fail to stress the contributions of Edgar Anderson and his followers to this field. A discussion of "Andersonian" techniques and their major consequence—introgression—would have given these chapters a more rounded coverage. The last three chapters deal with cytotaxonomy, the experimental categories, and an epilogue on the relationships between the "new" and the "old" taxonomy. A useful glossary and bibliography of significant monographs in the field conclude this, the primer of biosystematy.

For elaboration of the several themes outlined in the Heslop-Harrison book, the interested ecologist must inevitably turn to the Stebbins tome,[2] which by now (six years after its publication) is still the most cited reference work in modern plant evolutionary studies. Stebbins combines the intensive bibliographic approach (over 1300 literature citations) with his facile capacity for interpretation and synthesis. Thus the reader is given a kind of modern Darwin's treatment with masses of factual material liberally spiced with deductive analysis. The critical reader of Stebbins' work soon learns to recognize the often imperceptible shift from isolated facts to extrapolated generalization. These interpretive interludes should serve as challenges to further investigation, however, rather than to crabbed criticism of the authors' flights of speculation.

The plan of the book paraphrases the salient stages in evolution as espoused by most neo-Darwinists. Thus the first three chapters delve extensively into the analysis and description of variation at various hierarchical levels. Then, as Darwinian theory demands, natural selection follows, documented with some few detailed case histories. Documentary evidence (whether historical or experimental) of natural selection in plants is scanty, and Stebbins was undoubtedly hard put to present illustrative material for this chapter. A type of ecological research which might be called evolutionary autecology might well fulfill a vital need here, that of furnishing additional evidence for the existence and efficacy of natural selection in plants. A discussion of the Darlingtonian concept of the genetic system follows, emphasizing the dependence of the kind and rate of evolution (or speciation) on the nature of the genetic system. Speciation is then taken up in terms of kinds and degree of isolating barriers. Since genetic isolation has been a research specialty of Stebbins, we find his insight brought to bear on this subject, yielding the useful working hypothesis of *cryptic structural hybridity*.

Having accounted for the basic pattern of the evolutionary process in the first six chapters, Stebbins turns in the second half of his book to an analysis of some of the special processes that often distinguish plant from animal evolution. Inter- and intraspecific hybridization, polyploidy and apomixis are the three major evolutionary mechanisms exploited so extensively by plants. Of special interest to ecologists is Stebbins' analysis of introgressive hybridization, an evolutionary process that is largely triggered by ecological changes. Two chapters thoroughly explore polyploidy from cytological, genetic, and ecogeographical standpoints. Treatments of apomixis (the sexual "by-pass") and structural hybridity follow in the next two chapters and the final three chapters survey evolutionary trends and rates for the higher categories.

Long overdue is the active and universal recognition

[1] Heslop-Harrison, J. 1955. New concepts in flowering-plant taxonomy. London: William Heinemann Ltd.; Cambridge: Harvard Univ. Press. viii + 135 pp., 12 figs. 6s., $1.25.

[2] Stebbins, G. Ledyard, Jr. 1950. Variation and evolution in plants. New York: Columbia Univ. Press. xix + 643 pp., 9 tables and 55 figs. $8.00.

by plant ecologists of the genetic factor in ecological study. If the description of vegetation in associational terms is to have any objective reality, recognition must be given to genetic variation as a prime factor in differentiation of the facies of any plant community. The genetic concepts of population, race, and species, as well as the dynamics of their impermanence must be reckoned with in the ecologist's appraisal of vegetational units. No two individuals (of an amphimictic species) are alike genetically, and even more significantly, no two populations of amphimicts are genetically alike. The inclusion of analyses of different populations of the same taxon in ecological studies will be under a shadow of doubt until their genetic characteristics are known. Should the plant ecologist be convinced of this defect in his armametarium, he could do no better than to instruct himself on the concepts, techniques and phenomena associated with the synthetic discipline of biosystematy. These two books are "must" reading for all such enlightened ecologists!

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A Comprehensive Account of the Rattlesnakes[1]

Rattlesnakes, with two genera, 30 species, and 65 subspecies, occupy much of the New World. One species or another inhabits most of the region between southern Canada on the north and Uruguay and northern Argentina on the south, through 86 degrees of latitude. The more important of the two genera, *Crotalus,* is more widely distributed than any other group of reptiles in the Americas. Because they are venomous and equipped with a unique structure, the rattle, more attention has been devoted to the rattlesnakes than to any other group of reptiles in the Western Hemisphere. It is particularly fitting, therefore, that the outstanding herpetological work of the century should be devoted to them.

Not inaptly described on the dust jacket as "a compendium of everything that is scientifically known about rattlesnakes," these two volumes are the fruit of eleven years' work by a brilliant student of reptiles. Actually it is more than a compendium or even an "encyclopedia of the rattlesnake" as the author modestly describes it. For over and above that it is a critical, meticulous, and exhaustive study that integrates an almost unbelievable amount of information. Not only does it survey published accounts and summarize the author's voluminous studies and personal observations; innumerable bits of information have been gleaned from a formidable correspondence with field observers and naturalists throughout the United States.

In the hands of a less critical or judicious author much of the information obtained from field observers could have been misleading. As presented by Klauber it is an unusually competent survey of "both the rattlesnake's reactions to its environment and man's reaction to the rattlesnakes," something never before attempted. The immensity of the task, the thoroughness with which it has been carried out, and the extent of the coverage are unprecedented in the field of herpetology.

The style is extraordinarily lucid, with a skillful avoidance of unnecessary technical jargon. What has seemed complex in the words of other authors becomes almost deceptively simple as explained by Klauber. Information is conveyed in a stimulating, down to earth manner, but never sensationalized. Countless comparisons are made with other species and whole fields of knowledge are often reviewed in order to provide suitable background for the information pertaining to rattlesnakes. It would not be far-fetched to describe the work as a biology of snakes with emphasis on two crotalid genera. The bibliography, from which papers that merely cite locality records have been omitted, contains nearly 3,500 entries including many obscure references; this provides some idea of the exhaustive nature of the work.

It is doubtful whether any volumes were ever prepared with the needs of the user more constantly in mind. All data suitable for the purpose have been tabulated and there are innumerable cross references in the text. A vast amount of thought and effort was manifestly devoted to the index, which could have been unwieldy in a work of this sort. Those who will take time to read the foreword to the index will find that specific bits of information can readily be located in the text or tables.

Our knowledge of rattlesnakes, thanks to Klauber's efforts, now exceeds that for any other group of reptiles of comparable size. There are, of course, gaps in the record, and much more is known of the common species than of those with restricted ranges in remote regions in Latin America. Precise information concerning the habits and behavior of such secretive creatures as rattlers is difficult to obtain. The observations of field naturalists may leave something to be desired, but when integrated and interpreted by Klauber they provide the best information available concerning the behavior and activities of these reptiles.

Klauber displays the insight and understanding of his subject that can come only through long participation in a field of research that is at once specialized and diversified. For these two volumes cover the rattlesnakes from the aspects of the taxonomist, the psysiologist, the paleontologist, the immunologist, the ecologist, the ethnologist, the evolutionist, and even the student of folklore, to mention only a few. Of particular interest to ecologists are chapters dealing with Populations and Ecology, Hibernating Dens and Their Uses, Aggregations and Dispersal, Habitat Propensities, Island Habitats, and Food, but numerous other topics such as "scale characters and climate" are not without their ecological aspects.

The Berkeley Press deserves credit for an excellent job of editing, printing, and binding, with a simplicity of design on the cover that lends the book an air of distinction that it deserves. Readers so inclined will look in vain for something to criticize. Reviewers can only search their vocabulary for superlatives that have not become shopworn by their misuse in Hollywood or Madison Avenue.

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[1] Klauber, Laurence M., 1956. Rattlesnakes, their habits, life histories, and influence on mankind. Berkeley and Los Angeles: published for the Zoölogical Society of San Diego by the University of California Press. 2 vols.: vol. 1, pp. i-xxx, 1-708, 186 figs., 39 tables, frontispiece; vol. 2, pp. i-xviii, 709-1476, 57 figs., 19 tables, frontispiece. $17.50.

Evolution and Classification of the Mountain Caddisflies[1]

Three families of caddisflies, the Philopotamidae, Rhyacophilidae, and Glossosomatidae, are noteworthy because of their core of cool-adapted genera confined to mountainous areas. Dr. Ross has long been interested in their phylogeny, distribution, fossil evidence, and deduced dispersal pattern. In order to test the hypothesis that these three families arose from a cool-adapted ancestral form and subsequently underwent widely divergent speciation in many scattered geographical areas, he has rechecked the basic phylogeny of the entire order Trichoptera. Evolution up to the family level is considered primarily on the basis of structures of the larvae, pupae, and case-building habits; at the generic and species levels the adult structures are considered more important. The resulting phylogenetic tree has a number of innovations including the idea that *all* Trichoptera were cool-adapted up into early Cretaceous times but thereafter certain families, subfamilies, and genera appeared which were warm-adapted.

One long chapter is devoted to each of the three families which are considered in detail. Genitalia, wing venation, geographical distribution, avenues of dispersal, and ecological affinities are considered on a world-wide basis. Phylogenetic trees are constructed for many genera. As a consequence, numerous taxonomic changes are included, and there are descriptions of four new genera and 37 new species, as well as many new subgenera.

A short chapter entitled "Common Dispersal Characteristics" and a long chapter entitled "Dispersal in Geologic Time" are perhaps of greatest interest to the ecologist. The former summarizes numerous instances of isolation of species groups in the Philopotamidae, Rhyacophilidae, and Glossosomatidae with respect to mountain areas of all continents. Apparently there has been a repeated dispersal between certain mountain masses of the Northern Hemisphere. Although a trans-Atlantic dispersal probably never occurred, there are strong phylogenetic affinities between western North American species and northeastern Asiatic species. The latter chapter is a detailed and lucid correlation of evolution and dispersal patterns of the three families with the geologic time scale. It includes such items as Australasian dispersals, the Bering bridge, inter-American land bridges, and phylogenetic dispersal charts of several major genera.

This is a most remarkable entomological publication—done by our best student of the Trichoptera. It is especially noteworthy because it contains such a large proportion of original material and evidence meticulously gathered by Dr. Ross from many areas of the globe. It is impressive because he has logically and methodically deduced a thorough picture of the phylogenetic relationships of the genera and many species in these three families of caddisflies. This book is not for entomologists alone, but also for everyone interested in the fundamental problems of world-wide dispersal and zoogeography. It might well serve as an enviable model because of its clever integration of ecology, taxonomy, and evolution.

[1] Ross, Herbert H. 1956. Evolution and classification of the mountain caddisflies. Urbana: The University of Illinois Press. vi + 213 pp., 370 figs. and 45 charts. $6.00.

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Aquatic Insects of California[1]

Because of the exceptionally wide diversity of aquatic habitats within the boundaries of California, that state boasts an unusually large aquatic and semiaquatic insect fauna; and Dr. Usinger and 16 other specialists have done a remarkably fine service in treating this formidable phase of California biology. In addition to keys and descriptive material for all species known from the state, however, the book is all the more useful because it includes keys to all genera for the whole of North America.

General biology, ecology, habits, systematics, and collecting methods are discussed for each order and for many individual families. Keys cover both the imagoes and immature stages; in general, they are quite satisfactory and reasonably well illustrated. The average student, however, will experience some irritation because there are no page references in the keys. Pages 297 and 298, for example, contain keys to the families of beetles, but once a particular family has been run down in this key, the student must use the general index or page through the long beetle chapter until he comes upon the generic key for the family in question; and once he has run out his genus in this key, he must search further on in that chapter until he finds the species key for that genus.

The confirmed fresh-water biologist will be somewhat shocked to find that the book includes such oddities as semiaquatic Orthoptera, Dipsocoridae, several unusual hymenopteran families, Carabidae, Staphylinidae, and Melyridae. Discussions of intertidal zone insects are a welcome feature. The book is enhanced considerably by a long "Introduction to Aquatic Entomology" which is a refreshing and elementary discussion of limnology from the standpoint of aquatic insects. There is also a useful section on "Equipment and Technique," as well as a Glossary.

The pages are done in a wide, double-column format, and the printing is by offset. Most of the figures are borrowed, but almost all of those in the "Hemiptera" chapter are superb originals. Every serious American fresh-water biologist should make a place for this volume in his laboratory.

[1] Usinger, Robert L. (editor). 1956. Aquatic insects of California with keys to North American genera and California species. Berkeley and Los Angeles: University of California Press. ix + 508 pp. and numerous figs. $10.00.

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The Oceans and Man[1]

Although an alien medium, the sea plays a great part in the life of modern man. Its scientific investigation is still in relative infancy compared to the equivalent studies of land, yet it has had a great historical role in the growth of civilization and commerce and promises to have even greater influence in the future, when we know enough to be able to utilize its great food and mineral potential to the full. The very considerable increase in recent years of popular publications dealing with our scientific knowledge of the sea indicates a growing awareness on the part of the general public of the importance of the ocean and of ocean science to mankind.

With the growth of the various fields of oceanography it has come to be a meeting place of many kinds of specialists such as chemists, physicists, biologists, geologists and meteorologists, even electronic and acoustic engineers. Inevitably, many workers in the marine sciences will have little knowledge of this beyond their own field of specialization. Scientific workers, therefore, as well as the general reader may welcome an encyclopedic, well illustrated and non-technical publication concerning the ocean in all its aspects.

La Mer is not a scientific text book, but it is certainly encyclopedic and has much of interest for the student or scientist, thereby reflecting the scientific background of the marine biologists and oceanographers who have edited it. It also covers other topics of less scientific interest concerning the ocean in relation to mankind.

The text includes such diverse subjects as ancient legends and mythology of the sea, the history of oceanography, the prevention of shore erosion and the nature of deep sea sediments. One chapter is devoted to the topography of the sea bottom; another to the physical properties of sea water, sound propagation, light penetration and icebergs; one is given to the history of diving and submarine devices; other sections are concerned with waves, tides and currents, their origins and methods of measurement; the principal circulatory currents; ships and ports; the chemistry of sea water and its industrial application. The chapters on marine biology are divided into the pelagic flora and fauna and life on the sea floor. It is a mine of clearly written information.

Because of the wide scope of this book it is inevitable that each particular subject should be covered somewhat superficially. It is also to be expected that emphasis may seem unequally placed, depending, of course, on the reader's special point of view. Judged as an encyclopedia of the sea and its relation to man, however, it is excellent. In general form it is in keeping with the usual high standards of the publishers, Librairie Larousse. The diagrams are clear and attractive. It is profusely illustrated with well-chosen photographs which are excellent both pictorially and as illustrations of the context. Some of the 870 illustrations and 16 full page color plates are, in fact, magnificent. It is not surprising that in spite of its price it has become a best seller.

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[1] V. Romanovsky, Claude Francis-Boecef and Jacques Bourcart. With the collaboration of P. Bohé, J.-Y. Cousteau, Jean Fuega, M. Guierre and J. Peytel. 1953. La Mer. 503 pp., 16 color plates, 870 text figs. Paris: Librairie Larousse. 5200 fr., $13.50.

Soil Genesis in Geological History[1]

Soil genesis has been a topic of great interest to a wide range of scientists, including geologists and botanists, as well as pedologists. The viewpoint has grown up that soils are natural bodies with properties of their own, determined by climate, parent materials, biota, relief, and age of the surface. Since the days of Dokuchaev and Hilgard, geologists have tended to stand aside, and although interested, have left the development of the science of soils to pedologists. But slowly geologists have become aware that soils are, after all, a legitimate province for them. Now the author, a pedologist basically, produces a theory attempting to show the place of pedology in geology. He considers that pedogenesis is a phenomenon of equal importance to other natural phenomena which are studied in physical geology.

The author presents his ideas simply and attractively. The main thesis is that in past geological times there have been great periods of ecosystem stability, when forests were extensive, and landscapes relatively stable. He calls these periods the "Biotasie." During the *biotasie* phases, there was little erosion; and soil genesis proceeded steadily to produce a residual (e.g. lateritic) soil as a result of chemical translocation of elements. The rivers carry the alkalis, alkaline earths and silica to the sea. The *biotasie,* therefore, represents periods of accumulation of the translocated materials of the regolith in geological deposits, such as limestones and dolomites, and more or less silicified layers. The stage of disruption of the long-established forest equilibrium the author calls the "Rhexistasie." The *rhexistasie* phases in pedogenesis are correlated with the laying down of argillaceous and arenaceous sediments, conglomerates, bauxitic and ferruginous sediments, etc. as a result of the heavy erosion.

This main thesis after initial presentation is elaborated further, and discussed in four chapters. The first deals with the genesis of soils and sediments, paying especial attention to ancient sediments and sedimentation cycles. The succession of sediments in the sequences are considered to relate to soil-vegetation states, and to produce evidence for the "biorhexistasique" theory. The second chapter in elaboration discusses the duration of the geological periods and their causes in their relationship to *rhexistasie.* In the third chapter the theory is discussed relative to continental sediments like clays, bauxites and red sandstones. Finally, an interesting chapter summarizes the theory in terms of geochemical cycles and biological changes. Gigantism, extinction and the appearance of new species are all explained in terms of the sharply changing continental conditions suggested by

[1] Erhart, H. 1956. La genèse des sols en tant que phénomène géologique. Esquisse d'une théorie géologique et géochimique biostasie et rhexistasie. Paris: Masson et Cie. (Évolution des Sciences No. 8.) 90 pp. 560 fr., $1.65.

rhexistasie. The author proposes that climatic change is the main reason for the "bio-rhexistasie" cycles.

This is an interesting and well-written book with some very interesting ideas well worthy of further consideration. Many of them are not new, but the synthesis achieved is rather novel. The ideas and examples cover such a wide range that few will feel competent to make an immediate, over-all evaluation. There is little doubt, however, that a careful study of biological and geological data in relation to the theory should be made.

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Two Ecological Glossaries and a Proposal on Nomenclature

The field of ecology has a well-earned reputation for formidable, and sometimes excrescent, terminology. Many readers feel the need for a work defining the ecological terms they encounter; and to meet this need a well-known book, An Ecological Glossary[1] by J. R. Carpenter, has been reissued. Originally published in 1938, the book is now almost two decades old; and the fact that it cannot include more recent terms and shifts in meaning of older ones is an obvious limitation. The book includes, however, some 3,000 definitions; and many of these give citations of original uses or effective definitions in the literature. For professional ecologists it remains a very useful reference work, perhaps less for the definitions themselves than for these citations. For the non-ecologist who has occasion to read ecological literature, its value is more doubtful. Of a short list of currently important terms in English-language synecology and Continental phytosociology and biocenotics, the reviewer found that all but a few dated from before 1938 and were defined in the book. About half the definitions themselves, however, either were unclear or failed to give the most essential meaning of the term in current use.

A Dutch and Indonesian phytosociologist, E. Meijer Drees, has published another glossary[2] of about 1500 terms. Since it is in Dutch, and the terms are alphabetized in their Dutch forms, it is hardly for the general reader. The work may, however, complement the Carpenter glossary in a useful way: it is current, and it covers much more adequately the terms of Continental phytosociology. There is real need for a new glossary which will provide current, clearly stated definitions, preferably with citation of sources; and a beginning toward a new glossary has recently been made available by the Ecological Society.[3] The author or authors of a modern ecological glossary may well profit from the different and complementary glossaries of Carpenter and Meijer Drees.

Meijer Drees has also contributed to problems of terminology in another recent monograph[4, 5], discussing and defining many of the concepts of phytosociology. This work is by no means simply a review of Braun-Blanquet; a number of the ideas, notably the attempt to clarify the complex problems of character-species and to accept and deal with vegetational continuity, are the author's own. It includes also "A design for rules of phytosociological nomenclature"—i.e. rules for Latin naming and hierarchical classification of communities in the manner of the school of Braun-Blanquet. An issue of the journal VEGETATIO (Vol. 4, No. 4, 1953) has been devoted to an abridged English statement of these proposals and a discussion of them by other phytosociologists.

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[1] Carpenter, J. Richard. 1956 (reprinted from 1938). An ecological glossary. New York: Hafner Publ. Co. ix + 306 pp., 8 tables & 5 maps. $5.75.

[2] Drees, E. Meijer. 1951. Verklarende lijst van termen uit de plantensociologie en synoecologie. Rapport van het Bosbouwproefstation (Laporan balai penjeldikan kehutanan, Report of the Forest Research Institute), Bogor, Indonesia. No. 48 (Serie vegetatie-onderzoek No. 2): 1-140.

[3] Eggleton, F. E. et al. (Committee on Nomenclature of the Ecological Society of America). 1952. Report of the Committee on Nomenclature of the Ecological Society of America. 107 pp. Photographic copy available from J. L. Reed, Secretary of the Ecological Society of America, Department of Botany, University of New Hampshire, Durham, N. Hamp. $1.00.

[4] Drees, E. Meijer. 1951. Enkele hoofdstukken uit de moderne plantensociologie en een ontwerp voor nomenclatuurregels voor plantengezelschappen. Rapport van het Bosbouwproefstation, Bogor, Indonesia, No. 51 (Serie vegetatie-onderzoek No. 3): 1-218.

[5] ———. 1951. Capitata selecta from modern plant sociology and a design for rules of phytosociological nomenclature. (A summarized translation of the preceding.) Rapport van het Bosbouwproefstation, Bogor, Indonesia, No. 52 (Serie vegetatie-onderzoek No. 3A): 1-68.

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Bittmann, Ernst. 1953. Das Schilf (*Phragmites communis* Trin.) und seine Verwendung im Wasserbau. Angewandte Pflanzensoziologie [Stolzenau/Weser] **7**: 1-45, 12 figs., 48 photos. DM 3.90, $0.95.

Blinks, Lawrence R., L. Machlis, & J. G. Torrey, eds. 1956. Annual review of plant physiology. (Symposium) Palo Alto: Annual Reviews, Inc. 456 pp. $7.00.

Bobek, Hans. 1951. Die natürlichen Wälder und Gehölzfluren Irâns. Bonner Geographische Abhandlungen, Heft **8**: 1-62, 18 figs. and colored vegetation map.

Braun-Blanquet, J., H. Pallman, & R. Bach. 1954. Pflanzensoziologische und bodenkundliche Untersuchungen im schweizerischen Nationalpark und seinen Nachbargebieten. II. Vegetation und Böden der Wald- und Zwergstrauchgesellschaften (*Vaccinio-Piceetalia*). Komm. der Schweiz. Naturf. Gesell. zur Wiss. Erforsch. des Nationalparks, Ergebnisse der Wiss. Untersuch. des Schweiz. Nationalparks **4**(28): 1-200, 42 figs., 21 tables. 20 fr., $4.80.

Buchwald, Konrad. 1951. Bruchwaldgesellschaften im Grossen und Kleinen Moor Forstamt Danndorf (Drömling). Angewandte Pflanzensoziologie [Stolzenau/Weser] **2**: 1-46, 7 figs., colored vegetation map. DM 6.70, $1.60.

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Dobzhansky, Theodosius. 1956. The biological basis of human freedom. New York: Columbia Univ. Press. vi + 139 pp. $2.95.

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Guberlet, Muriel Lewin. 1956. Seaweeds at ebb tide. Seattle: Univ. Washington Press. xvi + 182 pp., numerous figs. $3.50.

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Haden-Guest, Stephen, John K. Wright, & Eileen M. Teclaff., eds. 1956. A world geography of forest resources. (Symposium) New York: Ronald Press Co. xviii + 736 pp., 167 figs and plates. $12.50.

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differentiation and growth. (Symposium) Princeton: Univ. Press. 236 pp., figs. $7.50.

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